Phylogeny of the wasp subfamily Metopiinae and patterns of speciation in the *Exochus albiceps* species-group

By

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Abstract

Metopiinae is a moderately large subfamily with over 850 described species distributed in 28 genera. The validity of Metopiinae had been doubted as they were suggested to be a derived member of the Ctenopelmatinae; and four genera—*Apolophus*, *Bremiella*, *Ischyrocnemus*, and *Lapton*—were only tentatively placed within the subfamily. Thus, there have been some doubts regarding the monophyly of the subfamily as currently circumscribed, whether the subfamily renders others paraphyletic, what genera should be contained within Metopiinae, and how these genera are interrelated.

The results presented here represent only a first step toward revising the systematics of metopiine wasps and creating a phylogenetically sound classification. The morphology-based phylogeny based on 101 terminal taxa (90 for the ingroup plus 11 outgroups) and 176 morphological characters, recovered Metopiinae as monophyletic, and sister to a clade formed by Tryphoninae, Mesochorinae, and Ctenopelmatinae. With respect to the four genera tentatively placed in Metopiinae, only *Scolomus* clustered well within the subfamily, while *Bremiella, Ischyrocnemis*, and *Lapton* were found as sister to the remaining metopiines, with their definitive placement remaining far from being resolved. Four main clades were recovered within the subfamily. The monophyly of most genera was recovered and with good support, and additional synapomorphies are proposed for several genera. However, in all the analyses *Stethoncus* was nested within *Hypsicera*; and the genus *Forrestopius* was not recovered as monophyletic, as *Forrestopius larryi* clustered within *Leurus*. Additionally, five new genera were found: *Finisterra* gen. nov., *Huetzin* gen. nov., *Jirajara* gen. nov., *Wira* gen. nov., and *Yanesha* gen. nov. The new genera inhabit high elevation regions of the Neotropical Region, areas that are poorly explored.

Base on this phylogenetic analysis of the subfamily, the monophyly of *Exochus albiceps* species-group was demonstrated. The monophyly of the *albiceps* species-group was well supported by morphological characters but poorly supported by the gene 28S, the combined molecular (28S, ND1, and Wg), and the combined molecular and morphological analyses. In addition to *E. albiceps* and *E. tegularis*, three species are newly assigned—*E. ablatus* Gauld & Sithole, 2002, *E. izbus* Gauld & Sithole, 2002, and *E. jacintus* Gauld & Sithole, 2002—and another six species newly described from the Neotropical region.

In order to investigate the spatial variation and niche requirements of the *albiceps* species-group, a climate-based modelling of species' niches was employed to estimate the level of niche overlap between species within the *E. albiceps* species-group, seeking to elucidate the relationship between elevational range and niche breadth. Segregation in the environmental space was found between species inhabiting the lowlands and the ones inhabiting montane regions. There is niche partitioning among the species that inhabit in montane regions while the lowland species occupied similar ecological space. The species show to have a narrow physiological thermal tolerance and are specialized for life at specific elevations.

Author's Disclaimer

Following the recommendation of Article 8 of the International Code of Zoological Nomenclature, taxonomic acts in this work are disclaimed for nomenclatural purposes.

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CHAPTER I: Introduction to the parasitoid wasps Metopiinae

Ichneumonid parasitoid wasps (Hymenoptera: Ichneumonidae) are among the most diverse and ecologically important groups of terrestrial organisms. They are well represented in all parts of the World, occurs from the Arctic to the tropics, but also from urban to agricultural ecosystems (Khalaim *et al*. 2012, Santos 2017). Ichneumonids have been suggested to be the largest of parasitoid families (Veijalainen *et al*. 2014), with approximately 24 000 described species (Yu *et al*. 2012) and over 100,000 estimated species (Gauld 1991), making Ichneumonidae the most speciose insect families (Gomez *et al*. 2017, Santos 2017).

Ichneumonidae are a well-established monophyletic group (Quicke *et al.* 2009, Santos 2017), but unravelling the classification of this huge family is a work in progress. In recent years, the number of subfamilies increased to 40 (Quicke 2015, Santos 2017). Its classification is gradually becoming fairly stable (Quicke 2015); nevertheless, it is likely that this number will increase as a more natural classification is achieved, particularly around the Ctenopelmatinae Förster, 1969 (Quicke 2015, Quicke *et al.* 2009). Systematic studies of Ichneumonidae have suggested that Metopiinae may have arisen from within the Ctenopelmatinae (Gauld & Wahl 2006, Quicke *et al.* 2009); suggesting that Ctenopelmatinae is not monophyletic and that this subfamily should be split or enlarged to encompass some other currently recognized subfamilies, such as Metopiinae Förster, 1969 and Mesochorinae Förster, 1969 (Quicke et *al.* 2009).

The doubt about the monophyly of Metopiinae arose with the placement of *Scolomus* Townes & Townes, 1950 (including *Apolophus* Townes, 1971, a junior synonym) within the subfamily (Gauld & Wahl 2006). *Scolomus* lacks the production of the dorsal margin of the face that is typical for metopiines; and some species possess a protibial apical tooth, a feature

that was consider an apomorphy for the Ctenopelmatinae (which is also present in Mesochorinae, and several other taxa outside Ctenopelmatinae) (Gauld & Wahl 2006). Their decision to transfer *Scolomus* to Metopiinae took in account the host record of *S. borealis* (Townes, 1971), a primary larval–pupal parasitoid of Lepidoptera as other metopiines (Broad & Shaw 2005).

The majority of Ichneumonidae develop, as larva, feeding on (ectoparasitoids) or in (endoparasitoids) other arthropods and finally kill the host (Gauld & Sithole 2002, Veijalainen *et al*. 2014). Metopiinae are solitary endoparasitoids of Lepidoptera, oviposition is into the host larva, but the emergence is from the host pupa (Bennett 2008, Gauld & Sithole 2002, Quicke 2015). Those species that lay eggs in concealed hosts are highly adapted to move around in tight spaces such as leaf rolls and tunnels, they possess short ovipositors and short, strong legs which may be pulled into mesosomal cavities, specialized head form and flanges for protecting important joints. (Gauld & Sithole 2002, Quicke 2015, Sääksjärvi & Bordera 2015).

Parasitoids play an important role in reducing the population density of their host (Veijalainen *et al.* 2014); and so, are key biological control agents of important pests in agricultural, forestry and natural ecosystems (Giunti *et al*. 2015). Many Metopiinae have been encountere das parasitoids of important forest and agricultural pest (e.g., Bennett 2008, Evenhuis & Vlug 1983, Moreau *et al.* 2010). Some species have been found as the most abundant parasitoids of a host, such as *Triclistus congener* (Holmgren, 1858) attacking the moth *Choreutis pariana* (Clerck, 1759) (Lepidoptera: Choreutidae) in apple orchards (Górska-Drabik 2003); while in other cases, they are not the most abundant but can attack several species, like *Exochus nigripalpis* Thomson, 1887 than has been reared from eight species of *Choristoneura* Lederer, 1859 (Lepidoptera: Choreutidae), a genus of moth that includes the most damaging forest pest in eastern Canada (Bennett 2008). But the most

common pest control agent in Metopiinae is *Hypsicera femoralis* Geoffroy, 1785, a European species that have been transported widely by human commerce as it is a parasitoid of stored-product lepidopteran (Townes & Townes 1959, Gauld & Sithole 2002).

Metopiinae (Fig. 1) comprise about 850 species and 28 genera (Khalaim *et al.* 2012, Yu *et al*. 2012), including the four genera—*Bremiella* Dalla Torre, *Ischyrocnemis* Holmgren, *Lapton* Nees, and *Scolomus*—tentatively placed in Metopiinae. The largest genera— *Exochus* Gravenhorst and *Metopius* Panzer—have a near world-wide distribution (Khalaim *et al.* 2012). The bulk of the richness is in the speciose genus *Exochus*, which comprises about ~290 species (Choi *et al.* 2016), and many more to describe from the Neotropical region (70 undescribed species from Peru, pers. obsv.). *Exochus* was found to comprise almost half of the Metopiinae species in most world regions (Gauld & Sithole 2002). Several less speciose genera are restricted to one region, such as the Afrotropical *Hemimetopius* Benoit (see Benoit 1955), the Neotropical *Cubus* Townes & Townes (Gauld Shithole 2002), the Nearctic *Bothromus* Townes & Townes (Walley 1966), among others.

Metopiines are well represented in all parts of the World, can be encountered in all habits from lowland forest to high elevation areas up to 4,100m (Chapter II). Though, the majority of species tent to inhabit between the lowlands and up to 1,600m, above this elevation species-richness declines (Gauld & Sithole 2002). At higher elevation several endemic taxa occur, such as the Neotropical genus *Forrestopius* Gauld & Sithole 2002 and four of the new genera encounter in this study (Chapter II).

Figure 1. Adults of various Metopiinae. **A.** *Pseudometopius hagenii*. **B.** *Exochus* sp. **C.** *Scolomus* sp. **D.** *Colpotrochia* sp. **E.** *Forrestopius* sp. **F.** *Seticornuta* sp. **G.** *Chorinaeus* sp. (scale bar=1mm).

The fauna of most regions only received limited attention. The only faunas for which Metopiinae have been thoroughly revised are the Nearctic (Townes & Townes 1959, Townes 1971) and Costa Rica (Gauld & Sithole 2002). These major revisions provided a picture of

composition of the subfamily but did not include any phylogenetic analysis, and only provided some informal comments about relationships between genera. Metopiinae, both taxonomy and phylogeny have, to date, only received limited attention. To understand Metopiinae diversification and test hypotheses about their evolution, robust phylogenetic hypotheses are need.

Quicke (2015) argued that one of the reason for the little attention was paid to the ichneumonoid wasps was the lack of reliable and accessible identification guides to the major groups and the fact that the subfamily-level classification is only now becoming stable. Due to recent efforts to elucidated relationships among the ichneumonide subfamilies (*Quicke et al.* 2005, Quicke *et al.* 2009), it is easier to target more specific questions, like the position of *Scolomus*, or if Metopiinae is a derived clade of Ctenopelmatinae or not, among others.

The present dissertation is aimed at investigating metopiine evolution, to understand diversification in metopiinae and test hypotheses about their evolution. The main goals for the Chapter II are to (1) test the monophyly of the subfamily Metopiinae; and (2) infer phylogenetic relationships among the genera, and (3) to test their monophyly. This was achieve by testing in a phylogenetical framework several hypotheses previously suggested: (a) that Metopiinae are not a derived group within Ctenopelmatinae, (b) that Metopiinae is monophyletic, (c) that the tentatively placed genera—*Apolophus*, *Bremiella*, *Ischyrocnemus* and *Lapton*—are metopiines, (d) that *Chorinaeus, Hemimetopius*, and *Trieces* are a natural group, (5) that *Colpotrochia*, *Cubus*, and *Triclistus* are a natural group, (6) that *Metopius* is a derived member of *Colpotrochia, Cubus*, and *Triclistus,* and (7) that all the genera are monophyletic. To test these hypotheses, I employed morphological-based phylogenetic analysis based on a comprehensive sampling of the genera, utilizing characters of the adults.

Based on the phylogenetic hypothesis for the subfamily Metopiinae and a good resolution of the genus-level classification obtained in the Chapter II, I selected a potential

monophyletic clade of *Exochus* to study in the Chapters III and IV. The aim of Chapter III was to test the monophyly of the *Exochus albiceps* species-group (*sensu*, Townes & Townes 1959) and infer the relationship among its species. To test this, phylogenetical analyses were performed using morphological data, molecular data, and in a combined analysis.

While gathering all the information of each species of the *Exochus albiceps* species-group (Chapter III), a disjunct distribution among the species was notice, some of the taxa are restricted to lowlands while other are distributed along the slopes of the Andes. Additionally, the *Exochus albiceps* species-group, at difference of other Neotropical Ichneumonidae, are commonly encountered and widely distributed (Gauld & Sithole 2002). This makes then a good test subject to explore niche modelling techniques. In the Chapter IV, I hypothesized that the species that inhabit the lowlands overlap their environmental niche but not with the species that inhabit on the montane slopes. To test this hypothesis, four environmental variables were model employing two R packages NicheROVER (Lysy *et al*. 2014) and Hypervolume (Blonder *et al.* 2014).

This research will permit for the first time a more accurate perspective on the species and morphological diversity within Metopiinae, a finer understanding of their distribution and ecological preferences, and allow for their identification by biologists and agronomists interested in further study of these wasps.

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CHAPTER II: Phylogeny of the subfamily Metopiinae (Hymenoptera: Ichneumonidae) based on morphological characters

INTRODUCTION

Metopiinae are a group of parasitoid wasps in the hyper-diverse family Ichneumonidae. The subfamily comprises about 850 species and 28 genera and are well represented in all parts of the world (Gauld & Sithole 2002, Khalaim *et al.* 2012). Metopiinae are solitary endoparasitoids of larval Lepidoptera (Quicke 2015). The hosts are either caterpillars that feed exposed on plants, or those that feed in weak concealment, such as in webbing and leaf rolls (Gauld & Sithole 2002, Townes & Townes 1959). In order to gain access to concealed hosts, many of the smaller metopiines use their short and robust legs which can be pulled into bodily recesses, the protracting convex anterior part of the head, and the well-developed flanges that protect critical joints to crawl within such confines and representing a suite of characteristics found in wasps that need to enter the narrow burrows or retreats of their hosts (Gauld & Sithole 2002, Quicke 2015).

Among Ichneumonidae, metopiines are one of the most easily distinguishable groups as most species have a distinctive habitus. Metopiinae are defined as stout-legged species, with a stout cylindrical body, with the clypeus not separated from the face by a groove, spiracles of the first abdominal segment at or in front of the segment's mid-length, the ovipositor short and not protruding beyond the end of the abdomen, and usually the second pro- and mesotrochanters fused with their corresponding femora (Townes & Townes 1959, Quicke 2015).

The concept of Metopiinae was formulated by Townes (1945), when he removed three tribes—Metopiini, Tylocomnini (*Spudaeus*), and Exochini—from the subfamily Tryphoninae. Subsequently, the genera assigned to Metopiinae were redefined by Townes

(1959) and Townes (1971), but four genera—*Bremiella*, *Ischyrocnemis*, *Lapton*, and *Scolomus*—have been placed within Metopiinae only tentatively and with hesitancy (Gauld & Sithole 2002, Quicke *et al*. 2005, Townes 1971). Relationships among metopiine genera has been poorly explored. The main tool to infer the position of the genera was the identification key for the world fauna proposed by Townes (1971), which mostly followed the "natural groups of genera" proposed by Townes & Townes (1959), but all based on an intuitive interpretation of character distributions. Subsequent to Townes (1971), three genera have been described: *Forrestopius* (see Gauld & Sithole 2002), *Ojuelus* (see Khalaim *et al*. 2012), and *Sciron* (see Fitton 1984). Several suggestions about relationships within Metopiinae were made by Gauld & Sithole (2002) in their study of the Costa Rican metopiines and by Fitton (1984) in his study of Australian metopiines, but again none were based on any critical analysis of character data.

The only phylogenetic analysis that included Metopiinae, all as part of the phylogeny of Ichneumonidae, included 20 metopiine genera with several genera represented by a single species, and with most of them, save for the exception of the uncertainly placed genera, were uniformly coded (Quicke *et al*. 2009). In their analyses, *Scolomus* was recovered as a metopiine in only a few topologies, while *Ischyrocnemis* never grouped with the other metopiines, and *Lapton* and *Bremiella* were clustered elsewhere within the Ophioniformes (Quicke *et al.* 2009), suggesting these four genera should be placed in their own monotypic subfamilies (Quicke 2015), or, at the least, outside of Metopiinae. Additionally, systematic studies of Ichneumonidae have suggested that Metopiinae may have arisen from within the Ctenopelmatinae (Gauld & Wahl 2006, Quicke *et al*. 2009, Quicke 2015).

The current state of affairs leaves some doubt regarding the monophyly of the subfamily as currently circumscribed, what genera should be contained therein, how these genera are interrelated, and whether or not the various genera are monophyletic. In the

present study, we present the first morphology-based phylogeny of Metopiinae based on a comprehensive sampling of the genera, utilizing characters of the adults. The main goals of this study were to: (1) test the monophyly of the subfamily Metopiinae; and (2) infer phylogenetic relationships among the genera of Metopiinae and test their monophyly.

MATERIAL AND METHODS

Specimens studied

The following acronyms are used to indicate entomological collections, followed by the curator's name:

CNC Canadian National Collection of Insects, Arachnids and Nematode, Ottawa, Canada (Andrew Bennett)

MNCR Museo Nacional de Costa Rica, Santo Domingo de Heredia, Costa Rica (Guisella Chávez Guevara)

MUSM San Marcos Natural History Museum, Lima, Peru (Diana Silva)

NHML Natural History Museum, London, England (Gavin Broad)

NHRS Swedish Museum of Natural History, Stockholm, Sweden (Hege Vårdal)

SEMC Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA (Michael. S. Engel)

UAT Insect Museum of Universidad Autónoma de Tamaulipas, Cd. Victoria, Mexico (Enrique Ruiz-Cancino)

UMSP University of Minnesota Insect Collection, Minneapolis, Minnesota, USA (Robin Thomson)

USNM United States National Museum, Washington D.C., USA (Robert Kula)

USUC Utah State University, Logan, Utah, USA (David Wahl)

Photomicrography

Photomicrographs were prepared using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscopic lens. Digital photos were combined by using the program CombineZP. Plates were prepared using Adobe Photoshop and Ilustrator CS3.

Selection of terminal taxa

One or several exemplar species were selected of each genus hypothesized by previous authors to belong to Metopiinae. The type species of 15 genera were included (see Appendix 1). When possible, we included multiple representatives of larger genera to sample the morphological diversity and test their monophyly, a similar approach was adopted for genera whose monophyly was in doubt. In most case both sexes were included when individuals were available. For taxa that was identified to genus level but not to the species level, as they may not fit to any of the currently known species as may be new species or for lack of means to corroborate their identity, were given a unique identifier (e.g. *Leurus* A9).

The ingroup comprises 90 species representing 28 genera of Metopiinae and 12 other taxa belonging to the subfamily whose identity to genus was uncertain, while the outgroup comprises six other subfamilies of the Ophioniformes (sensu Quicke *et al.* 2005): Anomaloninae Viereck, Banchinae Wesmael, Ctenopelmatinae, Mesochorinae, Ophioninae Shuckard, and Tryphoninae Shuckard. A list of taxa, with complete species names, and geographic distributions is given in Appendix 1. *Ojuelus juachicus* Khalaim & Ruíz-Cancino, 2012 and *Scolomus borealis* (Townes 1971) were coded using only the literature (Broad & Shaw 2005, Gauld & Wahl 2006, Khalaim *et al.* 2012), as specimens were not available for direct study.

Selection of morphological characters

This study was based on 176 discrete characters from the morphology of the adults, comprising 397 different states (listed below). Characters were delimited from external morphology (136 characters), male terminalia (20), and female terminalia (20). Several characters were previously considered in phylogenetic studies of Ichneumonidae (Klopfstein *et al*. 2011, Quicke *et al.* 2009, Quicke *et al*. 2005), in some cases they were modified or reinterpreted; while many were excluded for being not phylogenetically informative to the scope of the current analysis. Other characters included were used in prior generic treatments (Alvarado & Rodriguez-Berrio 2013, Fitton 1984, Gauld & Sithole 2002, Gauld & Wahl 2006, Townes & Townes 1959), while the many remaining features were newly discovered and first used in analysis of ichneumonids here. This information is included for each character in the list of morphological characters.

Most critical characters have been illustrated with photographs in order to facilitate identification of different character states and the discussion of their evolution (Figs. 2–7). Several illustrations exemplify multiple character states, which are highlighted with an arrow, with an indication of character numbers and applicable states given. Only one example of each character state is highlighted.

List of morphological characters and character state definitions, references and notes

Prosoma

0. *Antennomere 2, in lateral view, with distal end*: (0) perpendicular to longitudinal axis, (1) diagonal, more than 20^{o} to the longitudinal axis.
1. *Antennomere 2, in lateral view*: (0) more than 2.5 times as long as wide; (1) less than 2.0 times as long as wide.

2. *Antennomere 2, in lateral view, female*: (0) longer than wide (between 1.1–1.8 times as long as wide); (1) as long as wide; (2) wider than long. This character is applicable only if state 1 is present in the character 1.
3. *Antennomere 2, in lateral view, male:* (0) longer than wide (between 1.1–1.8 times as long as wide); (1) as long as wide; (2) wider than long. This character is applicable only if state 1 is present in the character 1.
4. *Antennomere 3, female*: (0) cylindrical; (1) subcylindrical, compressed.
5. *Mandible*: (0) bidentate; (1) unidentate; (2) tridentate. Character 5 of Quicke *et al.* (2009) but modified and the state 2 was added.
6. *Lower mandibular tooth*: (0) turned upwards; (1) turned under, i.e. reflexed; (2) directly below upper. Character 8 of Quicke *et al.* (2009).
7. *Lower mandibular tooth*: (0) parallel to upper tooth; (1) turned upwards (Fig. 2A). The state 1 was found only in the *Stethoncus* and it is potentially a synapomorphy for this clade.
8. *Mandible*: (0) weakly tapered, apex more than 0.5 times as long as wide base; (1) 0.4–0.5 times as broad as base; (2) less than 0.3 times as broad as base; (3) at least as wide as base. Character 14 of Quicke *et al*. (2005); it is measured, as suggested, before separation of distal teeth.
9. *Mandible with abductor swelling*: (0) at center (Fig. 2C); (1) next to upper corner (Fig. 2F).
10. *Mandible with condylar ridge*: (0) continuous (Fig. 2G); (1) interrupted and turned upwards (Fig. 2E). State 1 is potentially a synapomorphy for *Aceraspis*.
11. *Mandible with condylar ridge*: (0) more or less straight (Fig. 1D); (1) curved (Fig. 2K).
12. *Mandible next to condylar ridge:* (0) flat, more or less (Fig. 2G); (1) with a concavity along the ventral margin (Fig. 2F).

Figure 2. Details of the head. **A.** *Scolomus megallanicus.* **B.** *Synosis* sp. **C.** *Hemimetopius angulitarsis.* **D.** *Seticornuta terminalis.* **E.** *Aceraspis* sp2. **F.** *Leurus* A9. **G.** *Colpotrochia cincta.* **H.** *Finisterra* B9. **I.** *Spudaeus indigus.* **J.** *Leurus* sp. **K.** *Leurus* AEIC3. **L.** *Metopius pollinctorius.*

Figure 3. Details of the head. **A.** *Stethoncus* AEIC1. **B.** *Stethoncus* AEIC1. **C.** *Forrestopius* CNC7. **D.** *Colpotrochia* sp. **E.** *Spudaeus indigus.* **F.** *Periope aethiops.* **G.** *Exochus izbus.* **H.** *Hypsicera* sp. **I.** *Seticornuta* sp**. J.** Metopiinae C1. **K.** *Finisterra* B5. **L.** *Leurus caeruliventris.*

13. *Mandible, if with a concavity along the ventral margin:* (0) only on proximal half (Fig. 2K); (1) along entire ventral margin (Fig. 2J). State 1 was found in several species of *Leurus*.
14. *Upper edge of mandible with a diagonal groove extending from upper corner (from the condyle) to middle of mandible*: (0) without; (1) with (Fig. 2H). State 1 was found only in *Colpotrochia*, *Cubus*, *Finisterra*, *Ojuelus*.
15. *Upper edge of mandible with carina extending from condyle at middle:* (0) without; (1) with a carina (Fig. 2L). State 1 is only present in *Metopius dentatus*.
16. *Upper edge of mandible with a carina extending from condyle at middle*: (0) without setae along the concavity (Fig. 2L); (1) with (Fig. 2I).
17. *Number of maxillary palp segments, female*: (0) five; (1) four. State 0 is considered plesiomorphic in Ichneumonidae (Gauld 1985, Quicke *et al.* 2009). This is character 9 of Quicke *et al.* (2009) but modified and separated by sex.
18. *Number of maxillary palp segments, male*: (0) five; (1) four. State 0 is considered plesiomorphic in Ichneumonidae (Gauld 1985, Quicke *et al.* 2009). This is character 9 of Quicke *et al.* (2009) but modified and separated by sexes. State 1 is a synapomorphy for the clade formed by *Forrestopius larryi*, *Leurus* A9, and *Leurus* A10, potentially also for *Leurus xalifer*, but this species is only known of the type specimen which is a female.
19. *Maxillary palp segment 2, female*: (0) tubular; (1) swollen. It is considered swollen, if it appears do when compare with its other segments.
20. *Maxillary palp segment 2, male*: (0) tubular; (1) globular, more or less flattened anteroventrally. It is considered swollen, if it appears do when compare with its other segments.
21. *Maxillary palp segment 3, female*: (0) tubular; (1) globular.

22. *Number of labial palp segments*: (0) four; (1) three. This is character 10 of Quicke *et al.* (2009).

23. *Labrum:* (0) broadly exposed (Fig. 2H); (1) concealed (Fig. 2B). This is the character 11 of Quicke *et al.* (2009). *Periope* was coded as 0 but the labrum is slightly exposed; *Hypsicera* CNC1 has the labrum weakly exposed but was coded as 1.

24. *Clypeus and lower face*: (0) separated by groove (Fig. 2A); (1) not separated by groove (Fig. 2D). Lower face and clypeus confluent and not separated by an impressed groove is feature that defines metopiine (Gauld & Sithole 2002). *Metopius* has a clear demarcation of the clypeus due the ventral edge of the facial shield, and the facial shield is considered a secondary development of the usual metopiine state where there is no groove is coded as not separated (Quicke *et al.* 2009). *Scolomus magellanicus* Walkley, 1962, *S. vidiris* Townes & Townes, 1950, and *Periope auscultator* Haliday, 1938, have the clypeus weakly convex and distinguishable from lower face, so were coded as state 1; while *Wira luisi* new species and *Wira* C5 have also the clypeus convex but there is not a clear separation from the face, so were coded as state 0. This is character 13 of Quicke *et al.* (2009).

25. *Clypeus*: (0) without apical fringe of closely spaced setae; (1) with apical fringe of closely spaced setae. This is character 20 of Quicke *et al.* (2009).

26. *Clypeus, at the base of mandible*: (0) without longitudinal protuberance upwards from the clypeus to the tentorial (Fig. 2F); (1) with (Fig. 2G).

27. *Clypeus, preapically*: (0) without transverse ridge parallel with the margin (Fig. 2G); (1) with (Fig. 2E). State 1 is a synapomorphy for *Aceraspis*.

28. *Facial shield*: (0) without; (1) with (Fig. 2L). The facial shield was considered to be a secondary development of the usual metopiine state that is without a groove (Quicke *et al.* 2009). State 1 is a synapomorphy for *Metopius*.

29. *Groove between compound eye and mandible:* (0) without (Fig. 2I); (1) indicated as a change in sculpture (Fig. 2A); (2) distinct groove on whole length (Fig. 2J). This is character 16 of Klopfstein *et al.* (2011).

30. *Lower face with tentorial pit:* (0) not ending on an elevation; (1) on an elevation (Fig. 3J).

31. *Interantennal process of lower face separated from lower face by prominent transverse carina, in front of antennae:* (0) without; (1) with (Fig. 3B). *Aphanistes* and *Mesochorus* present a carina but the shape is different, so it was coded as 0.

32. *Lower face, laterodorsally, separate by a carina from toruli to compound eyes:* (0) without; (1) with (Fig. 3B). *Mesochorus* has a carina but the shape is different (straight) so but it is and coded as 0; while 1 is considered when the carina is turned backwards.

33. *Interantennal process of lower face*: (0) without (Fig. 2A); (1) with a projection between antennae (Fig. 2C).

34. *Interantennal process when lower face projected*: (0) only between antennae (Fig. 3I); (1) reaching to frons (Fig. 3D).

35. *Interantennal process of lower face projected when only between antennae, in dorsal view:* (0) without (Fig. 3H); (1) with a carina-like projection surpassing the toruli (Fig. 3G); (2) with a carina-like projection reaching to mid ocellus (Fig. 3E). State 1 is potentially a synapomorphy for *Exochus*.

36. *Interantennal process of lower face projected when present between antennae*: (0) into a more or less triangular projection (1) interrupted, more or less concave (Fig. 2B). Townes & Townes (1959) proposed this as a synapomorphy for *Synosis*.

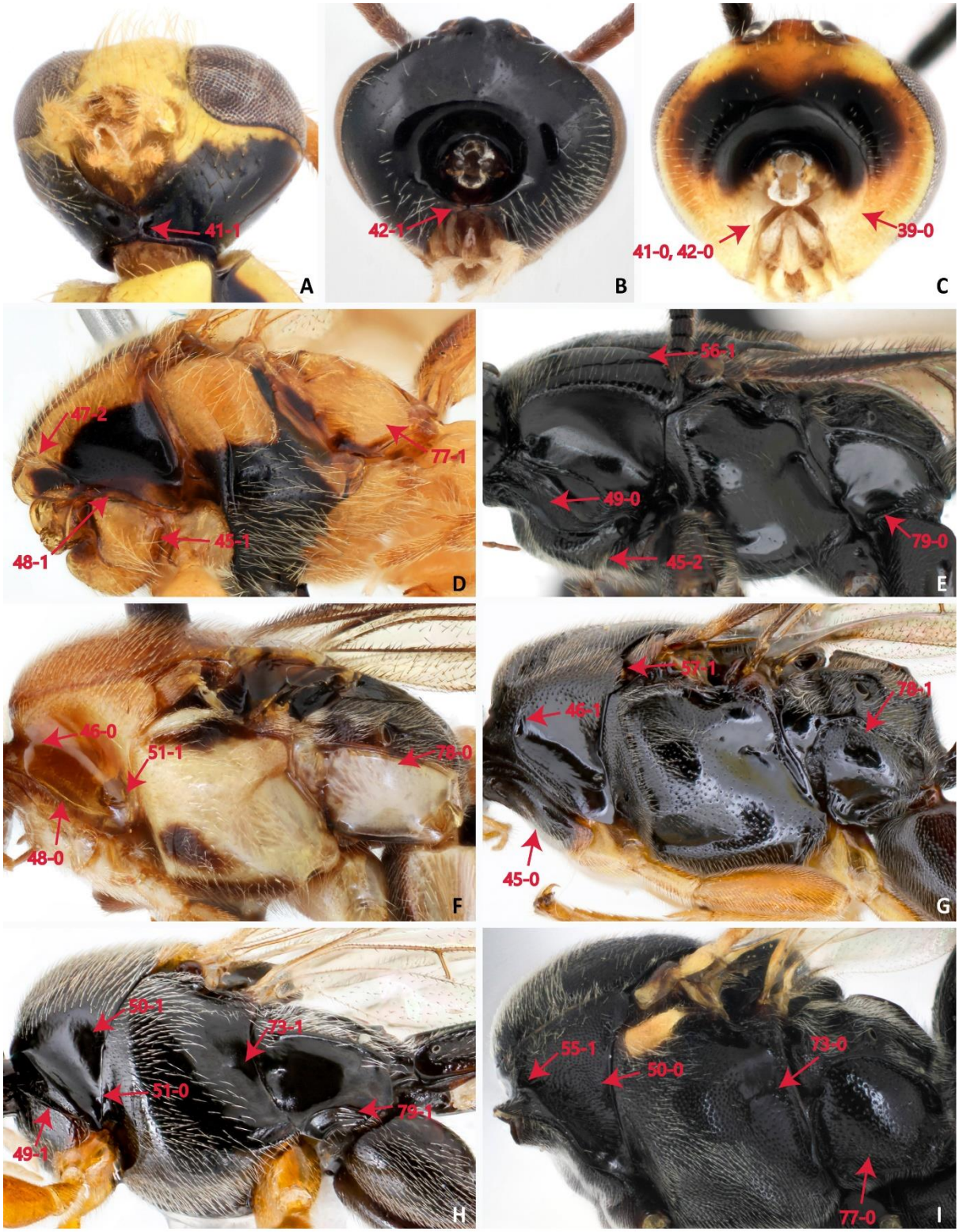

Figure 4. Details of head and mesosoma. **A.** *Cubus* sp. **B.** *Trieces peruanus.* **C.** *Exochus* sp. **D.** *Cubus* sp. **E.** *Stethoncus* AEIC1. **F.** *Seticornuta* sp. **G.** *Synosis* sp. **H.** *Trieces peruanus.* **I.** *Periope aethiops*.

Figure 5. Details of mesosoma. **A.** *Aceratapsis* sp2. **B.** *Scolomus megallanicus.* **C.** *Spudaeus indigus.* **D.** *Chorinaeus subcarinatus.* **E.** *Wira* C1. **F.** *Seticornuta albopilosa.* **G.** *Bothromus minoris.* **H.** *Hemimetopius angulitarsis.*

37. *Frons with a ridge surrounding the toruli*: (0) without; (1) with, when projection not reaches the frons (Fig. 3C); (2) with, meeting with the projection that reached to frons (Fig. 2F). The ridge is continuous from the lower face, it is located posterior to toruli.

38. *Frons with a ridge surrounding the toruli*: (0) complete (Fig. 3C); (1) interrupted at the middle (Fig. 3I).

39. *Frons integument, between toruli and compound eyes*: (0) without (Fig. 3E); (1) with striae (Fig. 3C).

40. *Occipital carina*: (0) complete; (1) dorsally absent; (2) ventrally absent; (3) absent; (4) dorsally and ventrally absent. This character was used by Gauld (1985); a complete occipital carina was considered when it is present along and joined to hypostomal carina, it is considered plesiomorphic. State 2 is added.

41. *Occipital carina when ventrally absent*: (0) otherwise (Fig. 4C); (1) turned inwards (Fig. 2K). This character coded as 1 is potentially a synapomorphy for *Finisterra*.

42. *Crease in similar position to occipital carina*: (0) without; (1) with (Fig. 3L). This character was taken from Gauld & Sithole 2002 and the state 1 was suggested to be present only in *Leurus*.

43. *Hypostomal carina with mid ventral line*: (0) absent, carinae separated from each other; (1) with mid ventral line, carinae in contact with each other (Fig. 4A). State 1 was found only in the *Cubus* and is a synapomorphy for the genus.

44. *Postgenal bridge*: (0) not projected (Fig. 4C); (1) projected (Fig. 4B). The state 1 was mentioned to be present in *Trieces* and *Metopius* (Gauld & Sithole 2002).

Mesosoma

45. *Propleuron*: (0) not cubical in profile (Fig. 4G); (1) almost cubical in profile (Fig. 4D); (2) almost subspherical (Fig. 4E). Propleuron cubical is consider a synapomorphy for *Cubus* (see Gauld & Sithole 2002).

46. *Pronotal epomia*: (0) absent (Fig. 4F); (1) present (Fig. 4G). Character 26 of Quicke *et al.* (2009).

47. *Pronotal epomia, shape*: (0) simple; (1) forming a long, sharp, raised ridge that is close to and more or less parallel with the anterior pronotal margin and reaches almost to the ventral corner of the pronotum; (2) produced dorsally joining and forming a flange, this flange separated from mesoscutum (Fig. 4D). This is character 27 of Quicke *et al.* (2009) but was modified and state 2 was added.

48. *Pronotum:* (0) with a shallow groove paralleling the anterior margin of the pronotum (Fig. 4F); (1) without (Fig. 4D).

49. *Pronotum, anteriorly:* (0) without (Fig. 4E); (1) with a distinctive section (Fig. 4H).

50. *Pronotum setae*: (0) homogeneously cover by setae (Fig. 4I); (1) with setae only in the upper margin (Fig. 4H).

51. *Pronotum, lower corner*: (0) without pocket-like structure (Fig. 4H); (1) with (Fig. 4F). The state 1 is present in most of the Metopiinae but some species of *Trieces* lack the pocket, this may be a consequence of a smoothing process, it was coded as state 0. *Metopius dentatus* Fabricius, 1779, *Spudaeus indigus* Davis, 1897, *Seticornuta albopilosa* Cameron, 1907, and *Seticornuta* form Guadalcanal have the pocket faintly defined and obscure by the striae but below the faint pocket there is a smooth section, they were coded as 1. *Scolomus megallanicus* and *S. viridis* are finely striate (not with wide striae as in *Aceraspis*, *Metopius*, and *Spudaeus*) in the lower half, but these striae reach to the lower corner of pronotum, and I coded as 0. *Alexeter innoxius* Cresson, 1879 and *Xenoschesis limata* Cresson, 1864 have some sculpture like carinae next to the distal section so it may look like it has a small concavity, so they were coded as 0.

52. *Pronotum with pocket-like structure:* (0) simple (Fig. 5F); (1) with a stria develop upwards anteriorly (Fig. 5E).

53. *Pronotum, integument*: (0) without striae; (1) with striae upper to pocket-like structure (Fig. 5A); (2) with striae centrally (Fig. 5F). *Carria dreisbachi* Townes & Townes, 1959 and *Sciron* sp. are coded as state 0, even though they have striae, but they are restricted to the area around the pocket; while state 1 is consider when striae are thick.

54. *Pronotum with upper margin*: (0) evenly convex (Fig. 5F); (1) with a shallow submarginal groove paralleled to upper margin (Fig. 5D); (2) with a deep groove next to upper margin (Fig. 4E). A shallow submarginal groove (state 1) was consider a putative autopomorphy for *Chorinaeus* but Gauld & Sithole (2002) reported many species of *Trieces* in Neotropical region also have this shallow groove.

55. *Pronotum with upper-anterior part*: (0) without a folded section; (1) with (Fig. 4I). State 1 was found only in *Periope*, it is potentially a synapomorphy for the genus.

56. *Pronotum with upper part*: (0) not exceptionally inflated; (1) inflated, so in dorsal view the pronotal lobe rapper as large triangular structures (Fig. 4E). Pronotum inflated was suggested to be a synapomorphy for *Stethoncus* (Gauld & Sithole 2002).

57. *Dorsal posterior corner of pronotum*: (0) slightly twisted and flattened (Fig. 5B); (1) weakly convex / rounded (Fig. 4G). This character is 28 of Quicke *et al.* (2009); when broadly rounded posteriorly, occluding the spiracular sclerite (Gauld & Sithole 2002)

58. *Dorsal posterior corner of pronotum*: (0) without longitudinal concavity; (1) with (Fig. 5C). State 1 was found only in the *Spudaeus* and it is potentially a synapomorphy for the genus.

59. *Propleuron with lower posterior corner*: (0) not produced or with only a small flange that does not touch or overlap pronotum (Fig. 5C); (1) produced as a lobe that touches

or overlaps the pronotum as a posteriorly directed ventral flange (Fig. 5F). This is character 29 of Quicke *et al.* (2009).

60. *Notauli*: (0) present, at least in part; (1) absent. This is character 30 of Quicke *et al.* (2009).

61. *Mesoscutum antero-laterally, next to pronotum*: (0) without concavity along the margin (it is scrobiculate); (1) with. State 1 was found only in the *Synosis* and it is potentially a synapomorphy for the genus.

62. *Mesoscutellum, at the middle*: (0) thinner than in the base (Fig. 6C); (1) as wide as at the base (Fig. 6A).

63. *Lateral ridges of mesoscutellum*: (0) only reaching over prescutellar ridge (Fig. 6C); (1) reaching to at least half the length of the mesoscutellum (Fig. 6B). Character is 29 of Klopfstein *et al.* (2011).

64. *Mesoscutellum with lateral ridges reaching at least half the length of the mesoscutellum*: (0) not expanded; (1) produced posteriorly into sharp processes (Fig. 6B).

65. *Mesoscutellum with lateral ridges produced posteriorly into sharp processes*: (0) continuous (Fig. 6A); (1) folded distally (Fig. 6B).

66. *Scutoscutellar groove*: (0) without (Fig. 6C); (1) with striae (Fig. 6D). Only laterally present in *Trieces bicalcaratus* Benoit, 1955, and with few striae in *Seticornuta* from Guadalcanal.

67. *Subalar prominence, shape*: (0) without an appearance of being folded over; (1) with (Fig. 5G). State 1 is a putative synapomorphy for *Bothromus* (see Townes & Townes 1959).

68. *Subalar prominence*: (0) convex (Fig. 5A); (1) flattened, with the appearance of the flange (Fig. 5D). State 0 was considered when is homogenously convex and the subalar

prominence is at least 0.3 times as wide as long; while the state 1 has the subalar prominence flattened and at most 0.2 times as wide as long. *Scolomus magellanicus* and *S. viridis* are coded as not applicable as the subalar prominence has thorn-shaped structure.

69. *Subalar prominence, basally*: (0) without a sharp out-curving spine; (1) with (Fig. 5B). State 1 is only present in *S. magellanicus* and *S. viridis*.

70. *Epicnemial carina*: (0) converging towards the anterior margin (Fig. 5C); (1) at the centre converging towards the posterior end (Fig. 5H). *Metopius dentatus* has the epicnemial carina short and interrupted at about the lower corner of pronotum, it is weakly converging towards to posterior end, so was coded as 1; other species of *Metopius* have the epicnemial carina converging towards the anterior end. This is character 34 of Quicke *et al.* (2009).

71. *Posterior transverse carina of mesosternum*: (0) complete; (1) present medially and laterally (absent in front of coxae); (2) absent or only present laterally. This is character 37 of Quicke *et al.* (2009).

72. *Posterior transverse carina of mesosternum, centrally*: (0) without finger-like processes; (1) with a pair of flattened finger-like processes; (2) with a pair of finger-like processes. The state 1 was found only in the *Cubus* and is potentially a synapomorphy for the genus.

73. *Mesopleural furrow*: (0) angled opposite episternal scrobe (Fig. 4I); (1) not angled opposite episternal scrobe (Fig. 5H). Character 35 of Quicke *et al.* (2009).

74. *Mesopleural suture:* (0) discernible (Fig. 5D); (1) not discernible (Fig. 5H). This character was taken from Gauld & Sithole 2002 and suggested that the state 1 is present only in *Trieces*.

75. *Mesopleuron on distal margin, anterior to mesopleural suture*: (0) scrobiculate (Fig. 5G); (1) smooth (Fig. 5D).

76. *Metapleuron division*: (0) with an evident sulcus (Fig. 5G); (1) without a sulcus, so seems flat (Fig. 5H). Pleural carina anteriorly turned down and reaching the anterior metapleuron and dividing metapleuron in upper and lower metapleuron.

77. *Metapleuron integument*: (0) cover with setae (Fig. 4I); (1) glabrous or with isolate setae (Fig. 4D). Large genera, like *Exochus* and *Trieces*, have species with and without setae.

78. *Metapleuron, upper margin*: (0) without (Fig. 4F); (1) with a band of setae along (Fig. 4G). State 1 was proposed by Alvarado & Rodriguez-Berrio (2013) as a synapomorphy for *Synosis*, but it is also present in *Stethonchus* and *Hypsicera*. *Stethoncus articus* has sexual dimorphism in this character, a fine line in female and is wider and with isolate setae in the upper half in male.

79. *Metapleuron, ventrally*: (0) without (Fig. 4E); (1) folded, in an analogous position to yuxtacoxal carina (Fig. 4H).

80. *Submetapleural carina*: (0) complete (sometimes as a narrow flange); (1) complete and strongly produced as a broad flange anteriorly. Character 39 of Quicke *et al.* (2009) but modified and the state 0 removed.

81. *Propodeal spiracle*: (0) elliptical or elongate (not more than 1.3 times as long as wide); (1) round or oval (less than 1.3 times as long as wide). Character 43 of Quicke *et al.* (2009).

82. *Anterior transverse carina of propodeum*: (0) present (Fig. 5B); (1) absent (Fig. 5H). State 0 was considered even when was faint or partially present only.

83. *Posterior transverse carina of propodeum*: (0) present (Fig. 5B); (1) absent (Fig. 5C). State 0 was considered even when was present between pleural and lateral longitudinal carinae.

84. *Lateral longitudinal carina of propodeum:* (0) absent, at most present after posterior transverse carina; (1) present. *Forrestopius* sp4 and *Yanesha chorui* sp.nov. has this carina faint but discernible, it was coded as state 1.

85. *Propodeum. lateromedian longitudinal carina*: (0) without, after posterior transverse carina; (1) with.

86. *Propodeum with lateromedian longitudinal carina after posterior transverse carina*: (0) widely separated (Fig. 6A); (1) convergent to a single carina (Fig. 6H).

87. *Forewing areolet*: (0) open; (1) closed by tubular or nebulous veins. Character 47 of Quicke *et al.* (2009).

88. *Forewing, areolet (when present)*: (0) quadrate (or triangular through anterior fusion of 2*rs-m* and 3*rs-m*); (1) pentagonal; (2) petiolate; (3) rhombic. Based on character 48 of Quicke *et al.* (2009), but the states 2 and 3 are added.

89. *Forewing, vein 2m-cu*: (0) with one bulla; (1) with two bullae. Character 50 of Quicke *et al.* (2009). The species of *Metopius* studied here present the state 1, but several species of the genus present the state 0 (Townes 1971).

90. *Number of basal hamuli of hind wing*: (0) two or more; (1) one; (2) none. Quicke *et al.* (2009) suggested that this character is not necessarily size-related within Ichneumonidae as there are a number of large ichneumonids with no basal hamuli (e.g. *Metopius*). Character 52 of Quicke *et al.* (2009).

91. *Number of distal hamuli of hind wing*: (0) seven to four; (1) eight or more. Character 54 of Quicke *et al.* (2009).

92. *Hind wing, intercept of Cu and cu-a (when present)*: (0) posterior to midpoint of *Cu* and *cu-a* (that is, closer to vein *A*); (1) at mid-point; (2) anterior to mid-point (that is, closer to vein *M*). Character 59 of Quicke *et al.* (2009).

93. *Fore and mid leg with trochantellus:* (0) clearly differentiated from femur; (1) not differentiated from femur.

94. *Fore leg with pretarsal claws*: (0) pectinate (with pecten of at least two teeth); (1) simple. Character 60 of Quicke *et al.* (2009).

95. *Fore-tibial spur, antero-dorsally*: (0) without comb or broad tract of setae; (1) with comb. Character 63 of Quicke *et al.* (2009), but I removed the state 2.

96. *Fore-tibial spur, postero-dorsally*: (0) without velum; (1) with velum. Character 64 of Quicke *et al.* (2009).

97. *Fore-tibial spur, postero-dorsally*: (0) with comb (either alone or posterior to velum); (1) without comb. This is the character 65 of Quicke *et al.* (2009).

98. *Apex of fore-tibia*: (0) without dentiform process; (1) with dentiform process. Character 66 of Quicke *et al.* (2009).

99. *Profemur*: (0) less than 0.25 times as wide as long (Fig. 6E); (1) more than 0.4 times as wide as long (Fig. 6F). The state 1 was found in most Metopiinae (except *Bremiella, Drepanoctomus, Ischyrocnemis, Lapton, Metopius, Pseudometopius*, some *Scolomus*, and *Spudaeus*).

100. *Profemur, ventrally:* (0) homogeneously convex; (1) with a concavity (Fig. 6F). *Metopius* is not evidently concave but flat but was coded as 1. State 1 was found in most Metopiinae and is a synapomorphy for the subfamily.

101. *Protarsomere 4:* (0) longer than wide; (1) wider than long. Gauld & Wahl (2006) suggest that this character occurs in most Metopiinae.

102. *Apex of mesotibia*: (0) without; (1) with dentiform process. This is character 66 of Quicke *et al.* (2009).

103. *Number of mid-tibial spurs*: (0) two; (1) one; (2) one in male, two in female. Character 69 of Quicke *et al.* (2009) but is modified and added the state 2.

104. *Mid-tibial spurs*: (0) inner longer than outer; (1) with equal length; (2) outer longer than inner. The length of the spurs was used by Gauld & Sithole (2002) to differentiate *Exochus*, *Forrestopius*, *Hypsicera*, and *Synosis*.

105. *Apex of metatibia*: (0) without; (1) with a dentiform process.

106. *Hind tibia with inner margin of apex*: (0) with comb; (1) without a comb. Character 72 of Quicke *et al.* (2009).

107. *Apical margin of hind tibial comb (when present)*: (0) straight or oblique; (1) curved. Character 73 of Quicke *et al.* (2009).

108. *Metatibia, laterally*: (0) evenly convex; (1) with a folding longitudinally (Fig. 6D). The state 1 was found only in *Hemimetopius* and it is potentially a synapomorphy for the genus.

109. *Metabasitarsomere, laterally*: (0) evenly convex; (1) with a folding longitudinally (Fig. 6D). The state 1 was found only in *Hemimetopius* and it is potentially a synapomorphy for the genus. This feature was mention in the description of *Hemimetopius angulitarsis* Benoit, 1955 (Benoit 1955a).

110. *Hooked lobe on the inner side of the distal metatarsomeres of female*: (0) without; (1) with (Fig. 6G). *Scolomus megallanicus* has a very small hook like projection.

Metasoma

111. *Spiracles of first metasoma tergite*: (0) behind mid-length; (1) anterior to or at mid-length. Character 77 of Quicke *et al.* (2009).

112. *Glymma of first metasomal tergite*: (0) absent; (1) sub-basal; (2) basal. Character 78 of Quicke *et al.* (2009).

113. *Suture between tergite and sternite of first metasomal segment*: (0) incomplete or absent; (1) complete. Character 79 of Quicke *et al*. (2009).

114. *Metasomal sternite 1, mid-point of posterior margin of anterior, more clerotized part*: (0) extending past middle of tergite; (1) not extending past middle of tergite. Character 80 of Quicke *et al.* (2009).

115. *Metasomal tergite I with lateromedian longitudinal carinae*: (0) weakly curved; (1) angulated.

116. *Metasomal tergite I*: (0) round or oval; (1) elliptical or elongate.

117. *Metasomal tergite I*: (0) at least as long as metasomal tergite II; (1) much shorter than metasomal tergite II. *Forrestopius larryi* has the metasomal tergite I, more or less, as long as tergite II, in lateral view looks like tergite II is longer; this species was code as 0. Character 81 of Quicke *et al.* (2009).

118. *Metasomal tergite I and II*: (0) free; (1) fused. This character was taken from Gauld & Sithole 2002 and suggested to be present only in *Metopius*.

119. *Basal thyridia of metasomal tergite II*: (0) present; (1) absent. Character 83 of Quicke *et al.* (2009).

120. *Basal thyridia of metasomal tergite II (if present)*: (0) transverse elongate adjacent to anterior end in short, wide depression; (1) circular or ovoid at anterior end in shallow depression. This is the character 85 of Quicke *et al.* (2009).

121. *Metasomal tergite II*: (0) at least as long as third tergite; (1) much shorter than third tergite. Character 90 of Quicke *et al.* (2009).

122. *Laterotergites of metasomal segments II*: (0) narrow; (1) large, at least 0.4 times as wide as long; (2) absent, apparently.

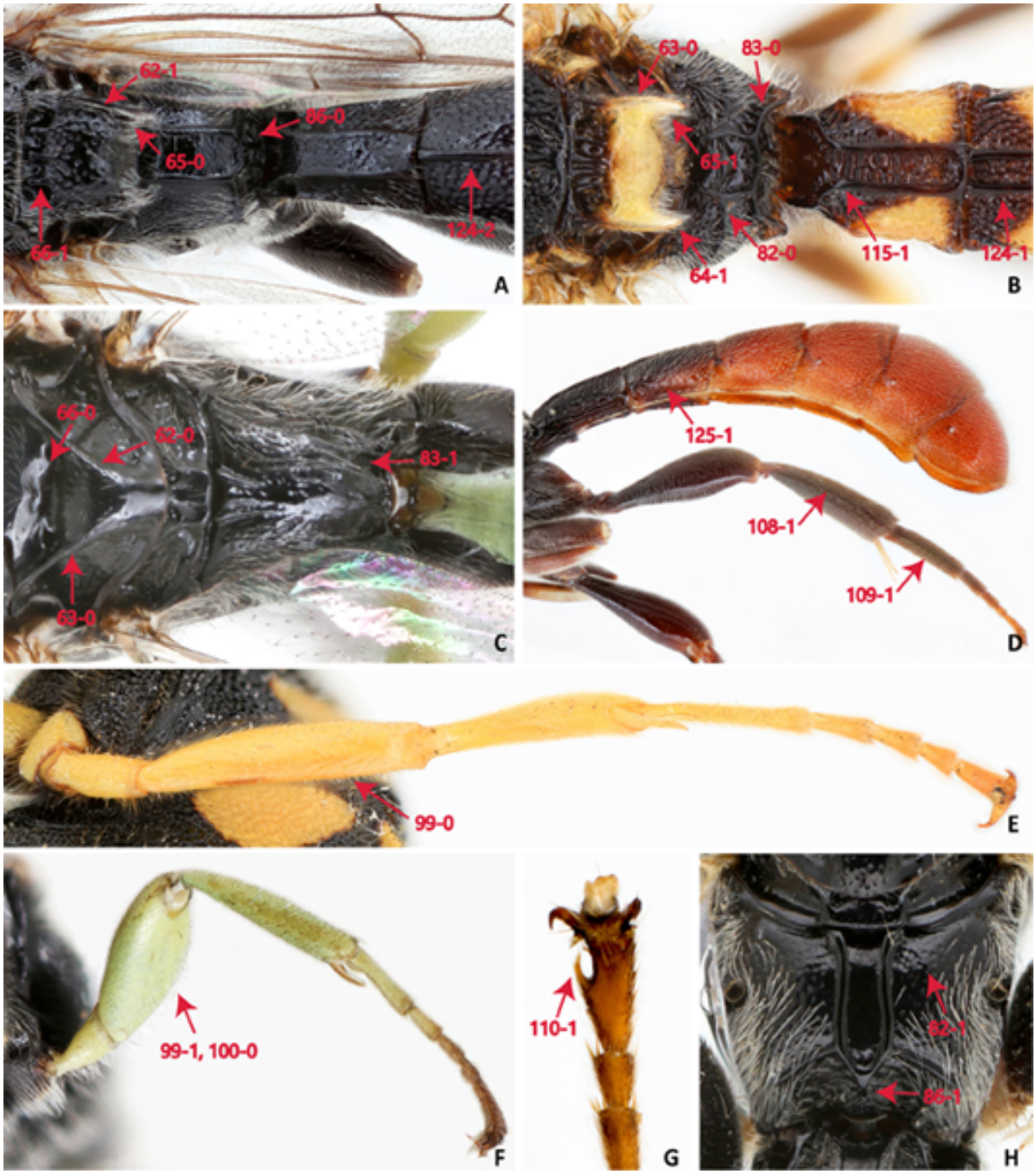

Figure 6. Details of head and mesoscutum, propodeum, metasoma, and legs. **A.** *Hemimetopius angulitarsis.* **B.** *Aceraspis* sp1. **C.** *Finisterra* B9. **D.** *Hemimetopius angulitarsis.* **E.** *Metopius dentatus.* **F.** *Finisterra* B9. **G.** *Triclistus* sp. **H.** *Leurus caeruliventris.*

123. *Metasomal tergite II*: (0) without grooves; (1) with anterolateral grooves. Character 88 of Quicke *et al.* (2009) but the state 2 was removed.

124. *Metasomal tergite II, development of lateromedian carinae*: 0) without; (1) with a pair carinae (Fig. 6B); (2) with a single carina (Fig. 5A).

125. *Metasomal tergite II, development of lateral longitudinal carinae*: (0) absent; (1) not exceeding anterior 0.4 of tergite (Fig. 6D); (2) exceeding the entire length of tergite.

126. *Metasomal tergite III of female*: (0) not as wide as high; (1) at least as wide as high. This is the character 91 of Quicke *et al.* (2009).

127. *Metasomal tergite III, development of lateral longitudinal carinae*: (0) without carinae; (1) with, at least on anterior 0.3 of the tergite length.

128. *Laterotergites of metasomal segments III and IV of female*: (0) neither laterotergite evenly or partially separated by a crease; (1) only laterotergite III at least partly separated by a crease; (2) both laterotergites at least partly separated by a crease. This is the character 92 of Quicke *et al.* (2009).

129. *Laterotergites of metasomal segments III and IV of male*: (0) neither even partly separated by a crease; (1) only laterotergite III at least partly separated by a crease; (2) both at least partly separated by a crease. Character 93 of Quicke *et al.* (2009).

130. *Metasomal laterotergite V (female)*: (0) not separate; (1) at least partially separated by a crease.

131. *Metasomal laterotergites III–VI*: (0) free; (1) folded under tergite. Metasoma with anterior five or six laterotergites not discernable, as they are folded and fused to the tergites.

132. *Tergite VI, distal margin*: (0) without; (1) with setae only on distal margin (Fig. 13C). *Colpotrochia cincta* Scopoli, 1763 has few setae and are arranged as in *Cubus*, *Finisterra* gen. nov., and *Triclistus*, so I code as 1.

133. *Metasomal tergite VI, with distal margin (Female)*: (0) without; (1) with a notch.

134. *Metasomal tergite VII, with distal margin (Female)*: (0) without; (1) with a notch.

135. *Tergite VI*: (0) simple; (1) hat-shaped, usually strongly sclerotized and covering tergite VII.

Characters of male terminalia

136. *Metasomal tergites VIII+IX of male, mediolaterally*: (0) not divided; (1) divided. This is the character 63 of Klopfstein *et al.* 2010.

137. *Metasomal tergites VIII+IX of male medially divided*: (0) not divided; (1) divided. *Leurus* sp 6 has the tergites VIII+IX partially divided basally and coded as 1.

138. *Paramere basally, in lateral view*: (0) less than 30^{o} (Fig. 7B); (1) more than 45^{o} (Fig. 7A). Measured as the angle form between the middle of the parameres and the most basal section.

139. *Paramere basally, in dorsal view*: (0) diagonal (Fig. 7E); (1) concave (Fig. 7K); (2) more less straight (Fig. 7C).

140. *Paramere basally, in dorsal view*: (0) fused; (1) separed (Fig. 7J).

141. *Paramere distally*: (0) flat (Fig. 7J); (1) turned, like a hood (Fig. 7F); (2) tubular.

142. *Paramere, in lateral view, with basal half*: (0) more or less diagonal (Fig. 7A); (1) with a convexity (Fig. 7B).

143. *Paramere, in lateral view, distally*: (0) otherwise (Fig. 7I); (1) slightly turned ventrally (Fig. 7A).

144. *Paramere, in lateral view, with distal half (ventrally)*: (0) convex; (1) more or less angled.

145. *Paramere, in ventral view, with margin pre-apically*: (0) slightly convex (Fig. 7E); (1) with a concavity; (2) straight (Fig. 7L).

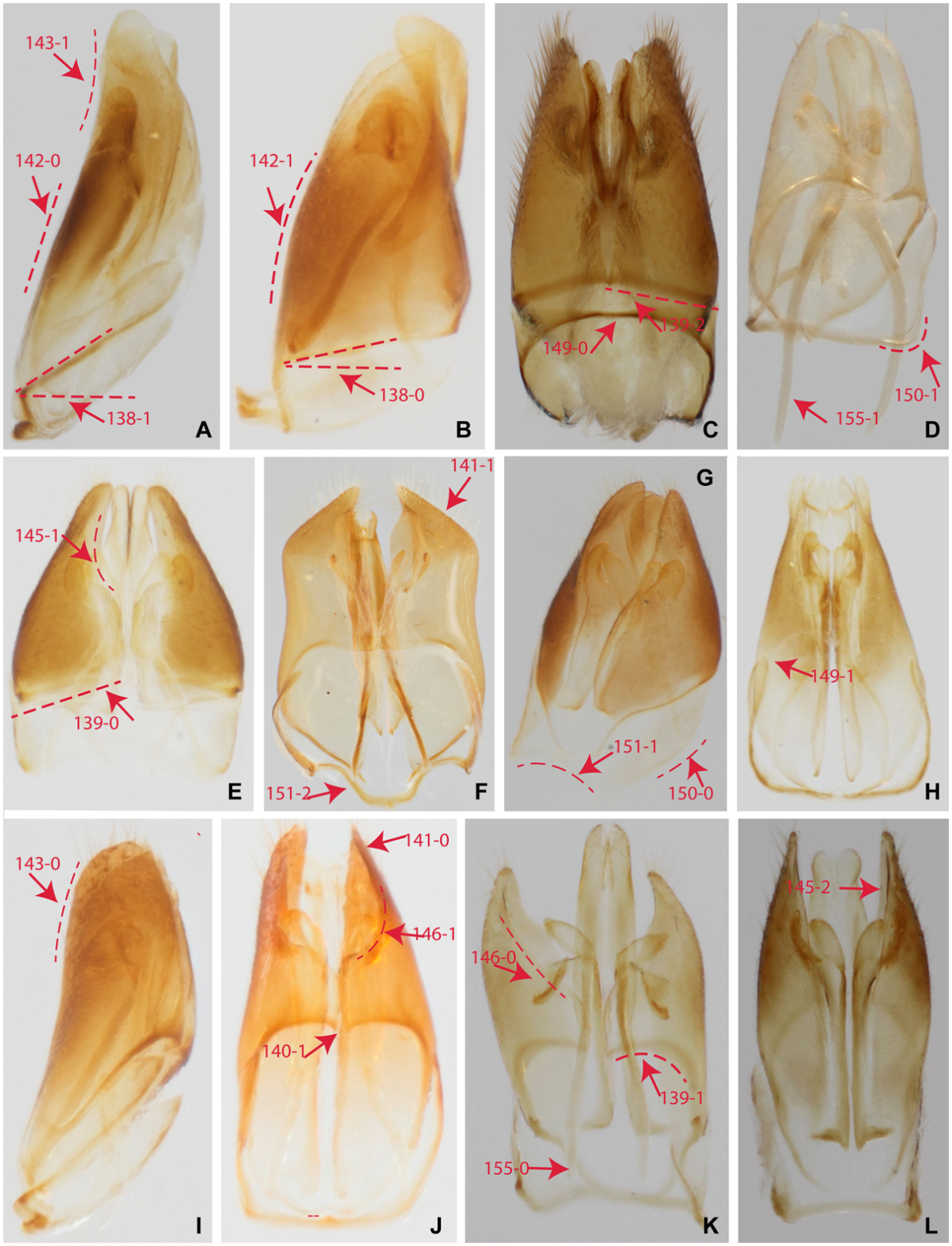

Figure 7. Details of male genitalia A. *Wira luisi.* **B.** *Phobetes* sp. **C.** *Aphanistes cachil.* **D.** *Colpotrochia* sp. **E.** *Phobetes* sp. **F.** *Metopius* sp. **G.** *Phobetes* sp. **H.** *Wira luisi.* **I.** *Leurus discus.* **J.** *Leurus discus.* **K.** *Trieces* sp. **L.** *Trieces horisme.*

146. *Paramere, in dorsal view, with inner margins*: (0) more or less straight (Fig. 7K); (1) with a concavity at the middle (Fig. 7J). *Chorinaeus californicus* Ashmead and *Chorinaeus cristator* Gravenhornst, 1829 look like concave but the tegument is folded over so was coded as 0.

147. *Paramere, in dorsal view, with inner margins with a concavity*: (0) only basally; (1) with a concavity in semicircular shape. State 1 is uniquely found in *Sciron*.

148. *Paramere, in dorsal view, with inner margins folded over*: (0) without; (1) with.

149. *Basal ring or gonobase, dorsally:* (0) complete (Fig. 7C); (1) interrupted (Fig. 7H).

150. *Basal ring or gonobase, ventrolaterally*: (0) without angulation (Fig. 7G); (1) with angulation (Fig. 7D). *Enicospilus flavoscutellatus* has a small angulation but it is not like the one present in Metopiinae, is less conspicuous, and not thickened.

151. *Basal ring or gonobase, ventrally, at center*: (0) oval or more or less straight; (1) curved inwards (Fig. 7G); (2) sinuate (Fig. 7F); (3) curved outwards.

152. *Male hypopygium (sternite 8) with lateral margins*: (0) parallel to each margin; (1) converging distally.

153. *Male hypopygium (sternite 8)*: (0) between 1/2–1as long as wide; (1) wider than long, not enclosing genital capsule; (2) longer than wide.

154. *Male hypopygium (sternite 8) distal end*: (0) continuous; (1) emarginated; (2) projected centrally. The character state 2 is uniquely found in *Seticornuta*.

155. *Apodeme of aedaegus*: (0) shorter than aedeagus (Fig. 7K); (1) longer than aedeagus (Fig. 7D).

Characters of female terminalia

156. *Sternite IV*: (0) weakly sclerotized, with membranous areas; (1) strongly sclerotized, sometimes with distal margin membranous. *Triclistus* and *Finisterra* may have the

distal margin less sclerotized but never membranous. This is the character was suggested to be present in *Triclistus* by Gauld & Sithole (2002).

157. *Sternite V*: (0) weakly sclerotized, with membranous areas; (1) strongly sclerotized, sometimes with distal margin membranous. *Macromalon* is posterior-centrally weakly sclerotized so it looks as notched.

158. *Sternite VI*: (0) weakly sclerotized, with membranous areas; (1) strongly sclerotized. *Drepanoctomus* and *Spudaeus* have the sternite VI strongly sclerotized but it is basally and/or distally membranous, so were coded as 0.

159. *Sternite VI*: (0) longer than wide (at most 0.9x as wide as long); (1) wider than long (at least 1.1x as wide as long). *Trieces horisme* Gauld & Sithole, 2002 is as long as wide, but I coded as 0.

160. *Sternite VI, basally*: (0) more or less straight; (1) strongly concave; (2) weakly concave; (3) inverted triangle.

161. *Sternite VI, distally*: (0) more or less straight; (1) ploughshare-shape, but laterally concave (Fig. 13C); (2) ploughshare-shape, but laterally convex. *Seticornuta* is softly convex, was coded as 0. This is the character 104 of Quicke *et al.* (2009), modified and the state 1 was removed and the state 2 was split in two.

162. *Sternite VI, if ploughshare-shape but laterally concave, distally*: (0) convex; (1) notched mid-posteriorly (Fig. 13C). The character 105 of Quicke *et al*. (2009) is modified.

163. *Sternite VI, mid-posteriorly*: (0) simple, but sometimes membranous apically; (1) notched mid-posteriorly. Character 105 of Quicke *et al.* (2009) is modified.

164. *Apodemes of metasoma tergite VI*: (0) shorter than their medial width; (1) longer than their medial width.

165. *Apodemes of metasoma tergite VI, distally*: (0) flattened; (1) tapering to the end; (2) clubbed at the end.

166. *Metasomal tergite VI, basally*: (0) without (1) with a distinct section.

167. *Tergite VII*: (0) not folded; (1) folded.

168. *Gonocoxite 9*: (0) with a lobe that extends past the insertion of the ovipositor sheath; (1) without. Character 109 of Quicke *et al*. (2009).

169. *Ovipositor, portion protruding beyond apex of metasoma*: (0) short (< 0.3 length of metasoma); (1) long (< 1.0 > 0.3 length of metasoma); (2) very long (> length of metasoma). Character 113 of Quicke *et al*. (2009).

170. *Base of dorsal ovipositor valve*: (0) abruptly expanded; (1) evenly expanded. Character 114 of Quicke *et al.* (2009).

171. *Base of ovipositor valve dorsally*: (0) without a weakly sclerotized zone; (1) with. Character 115 of Quicke *et al*. (2009).

172. *Metasomal tergite VIII*: (0) rounded (1) compressed dorsal-ventrally.

173. *Metasomal tergite VIII, dorsolaterally*: (0) not folded, neither partly separated by a crease (1) folded and separated by a crease. The state 1 was found only in the *Metopius* and is potentially a synapomorphy for the genus.

174. *Metasomal tergite VIII, dorsally*: (0) without; (1) with a concavity. The state 1 was found only in the *Synosis* and is potentially a synapomorphy for the genus.

175. *Metasomal tergite VIII, dorsally*: (0) not divided; (1) divided medially.

Phylogenetic analysis

A data matrix of 101 terminal taxa (90 for the ingroup plus 11 outgroups) and 176 morphological characters was compiled for this phylogenetic analysis (Appendix 2). All characters (either binary or multistate) were coded in Mesquite 2.75 (Maddison & Maddison

2010) and treated as unordered and unweighted. Character states of species for which genitalia or one of the sexes could not be examined (because of insufficient material or because females or males are unknown for these species) were scored with '?' and treated as missing data, while an en-dash (–) was used when that character was not applicable. Characters were polarized by outgroup comparison, under the assumption that the set of character states possessed by the outgroup is the best approximation of the plesiomorphic condition while the suite of character states possessed by the ingroup is apomorphic (Wiley & Liebermann 2011).

Parsimony

Searches for the most parsimonious trees (MPTs) were conducted using the heuristic 'New Technology search' algorithm of TNT using equally weighted (EW) settings (Goloboff & Catalano 2016), with 10,000 random addition sequences; heuristic searches were performed using multiple tree bisection and reconnection (TBR) branch swapping, holding 100 trees during each replication. Character state changes were mapped onto the tree using Winclada 1.00.08 (Nixon 2002). As more than one most parsimonious tree was obtained, a strict consensus tree was calculated (Goloboff *et al.* 2003). To evaluate branch support, Bootstrap (BS) and Jacknife (JS) support values were calculated using TNT (Goloboff *et al.* 2003), and the values were mapped onto the internal nodes of the tree (Fig. 9), BS sequenced JS.

Bayesian inference

Bayesian inference methods were applied using MrBayes 3.2.6 (Ronquist *et al*. 2012), analyzed under the MK model proposed by Lewis (2001) and implemented through the CIPRES platform. The analysis was run with two chains, for 10 million generations without a

stop rule. Trees values were sampled every 1,000 generations and probability values were sampled every 500 generations. Posterior probabilities (PP) of the nodes are reported on the 50% majority rule tree (Fig. 9). The output statistics of the Bayesian analysis were viewed in Tracer v1.6.0 (Rambaut *et al*. 2018) to evaluate the validity of the results. The criteria for evaluating the confidence were the standard deviation split frequencies (SDSF) under the standard value of 0.01, and the effective sample size (ESS) values of the average log normal likelihood (LnL), log normal probability (LnPr), and tree length (TL) to access whether the entire tree landscape was searched thoroughly enough. Trees were visualized and arranged in Figtree (v. 1.4.3), exported in PDF format, and edited in Adobe Illustrator CS3.

Phylogenetic signal

We assessed the phylogenetic signal of characters and determined the level of homoplasy among character sets by comparing the median value of retention index (RI) per character set and by conducting partitioned phylogenetic analyses. We grouped characters by tagmata (pro-, meso-, and metasoma), sex (male and female characters), and terminalia (male and female characters). We conducted partitioned analyses in TNT using the settings for equally weighted analyses under parsimony as indicated above. For each analysis, we recorded the number of MPT and tree statistics: tree length (TL), consistency index (CI), and retention index (RI).

RESULTS

The analyses were well resolved and the relationships within Metopiinae were recovered with good support on average. The parsimony analysis resulted in eight MPTs (TL = 744, CI = 29, RI = 76), with 10 collapsed nodes in the consensus tree (Figs. 8, 11, 12). The Bayesian analysis reached 10 million generations in 2 hours 17 mins 10 seconds (minimum

SDSF: 0.005738). The ESS values were high enough to consider this analysis converged (LnL: 5465, LnPr: 856, TL: 718). The strict consensus tree analysis is presented in Figure 9.

There were some discrepancies between the results of the different analyses (for comparison purposes the two trees are presented in Fig. 10). The parsimony analyses were generally better resolved than the Bayesian analysis; the topology of the trees was different especially in the nodes with low support, but the node support was higher in the Bayesian analysis. We therefore based this discussion on the parsimony analysis and only point out some important differences in the Bayesian analysis. The character-state changes were mapped on the strict consensus tree of parsimony analysis and are presented in the Figure 11 and 12. In the text, when the homoplasies are mentioned are only referred with the character-state number.

The topology of the outgroup taxa was consistent with current recognized taxonomic placements in Ichneumonidae based on previous phylogenetic results (Quicke *et al*. 2009). This study provides additional corroboration to the Upper and Basal Ophioniformes (*sensu* Quicke *et al*. 2009). The Basal Ophioniformes (Fig. 11) are supported by two unreversed synapomorphies: suture between tergite and sternite of first metasomal segment complete (113-1) and basal ring or gonobase, dorsally interrupted (149-1), and ten reversed synapomorphies: 94-1, 97-1, 107-1, 111-1, 112-1, 114-1, 128-2, 129-2, 137-1, and 150-1. The Basal Ophioniformes have high support (BS=100, JS=100, PP=1).

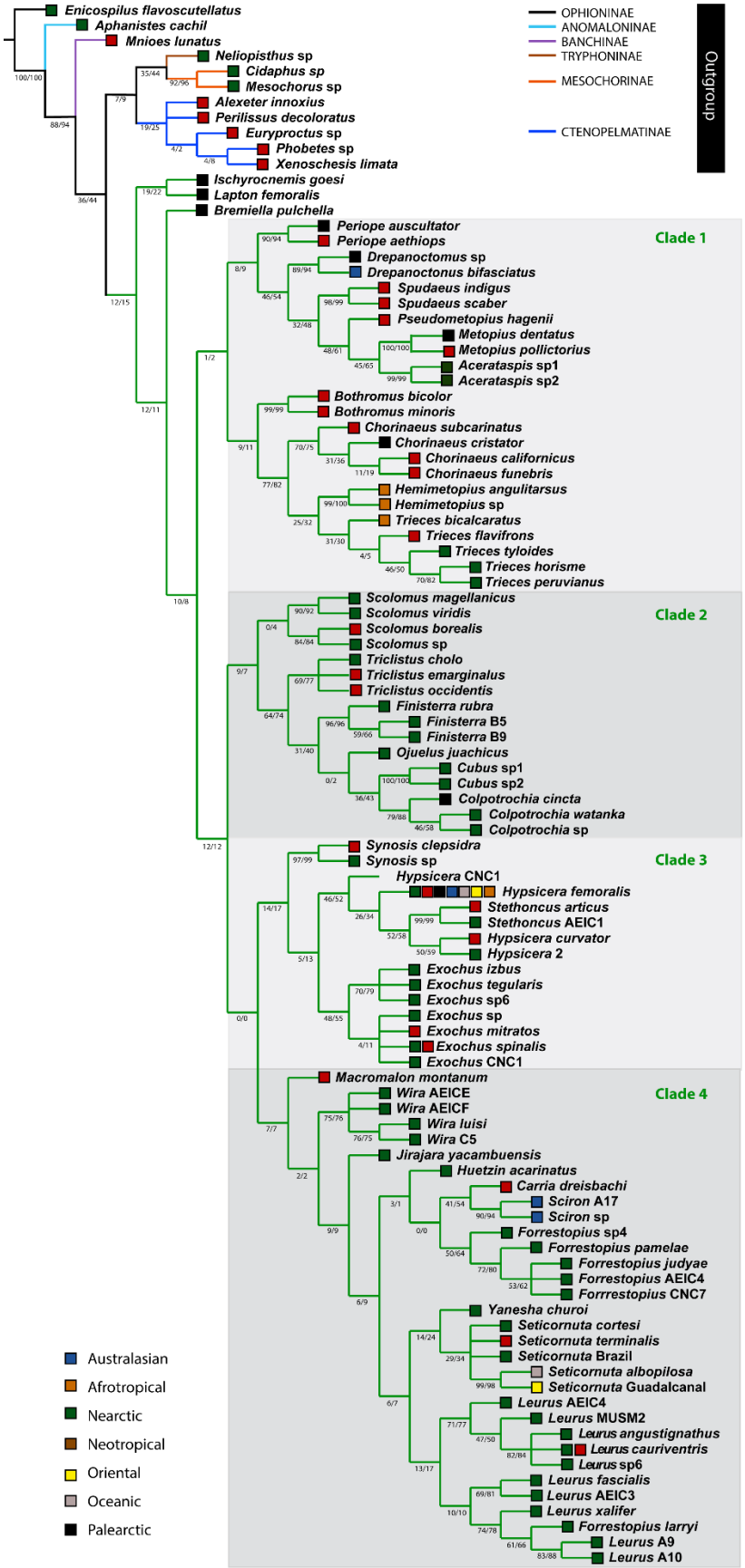

Figure 8. The strict consensus tree of eight equally most-parsimonious. Branch support values are displayed below the nodes in the following order: Bootstrap and Jacknife values. When no value is shown it refers as values could not be estimated.

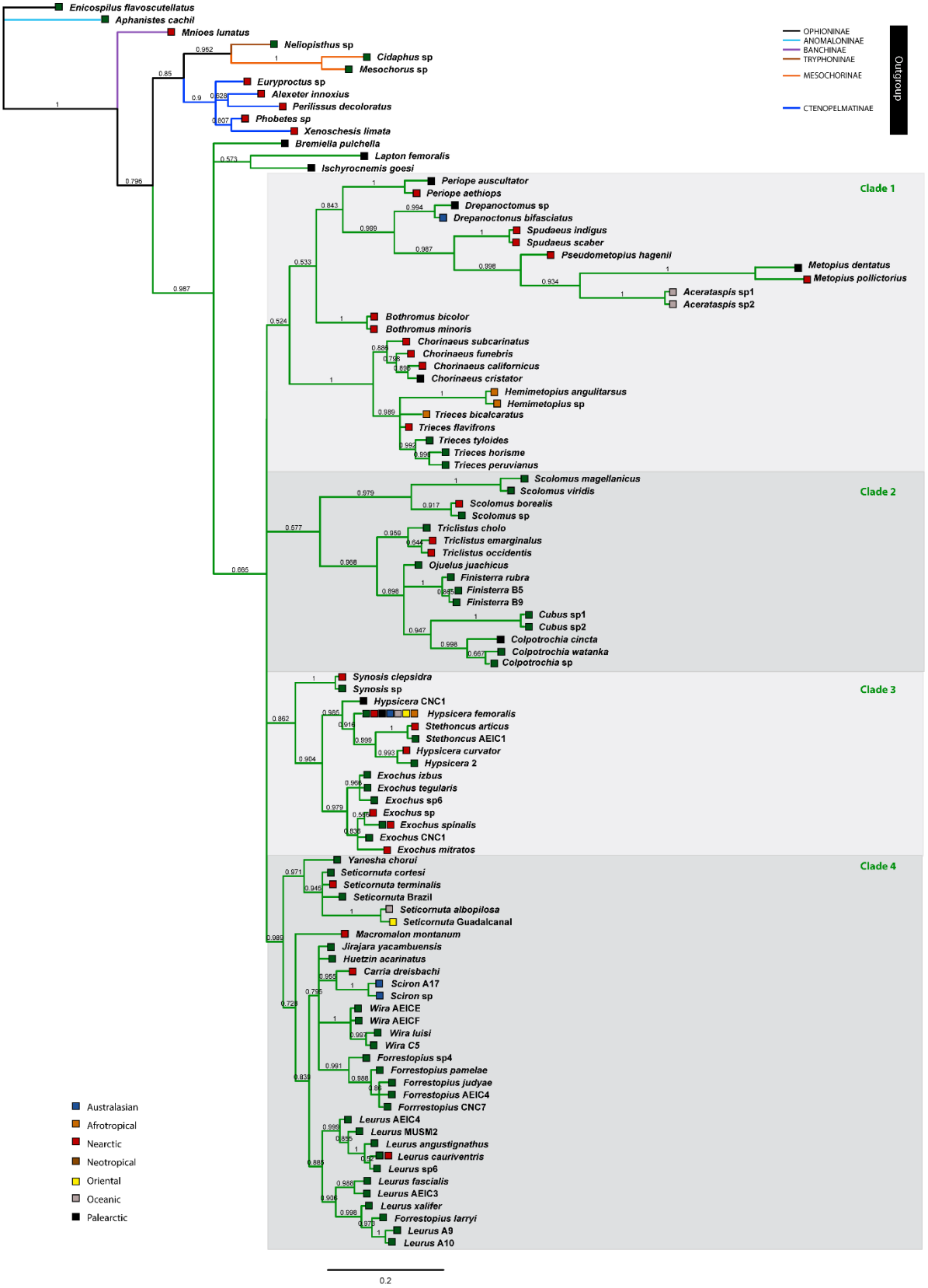

Figure 9. The strict consensus tree of the Bayesian analysis. Posterior probabilities values are displayed above the branches.

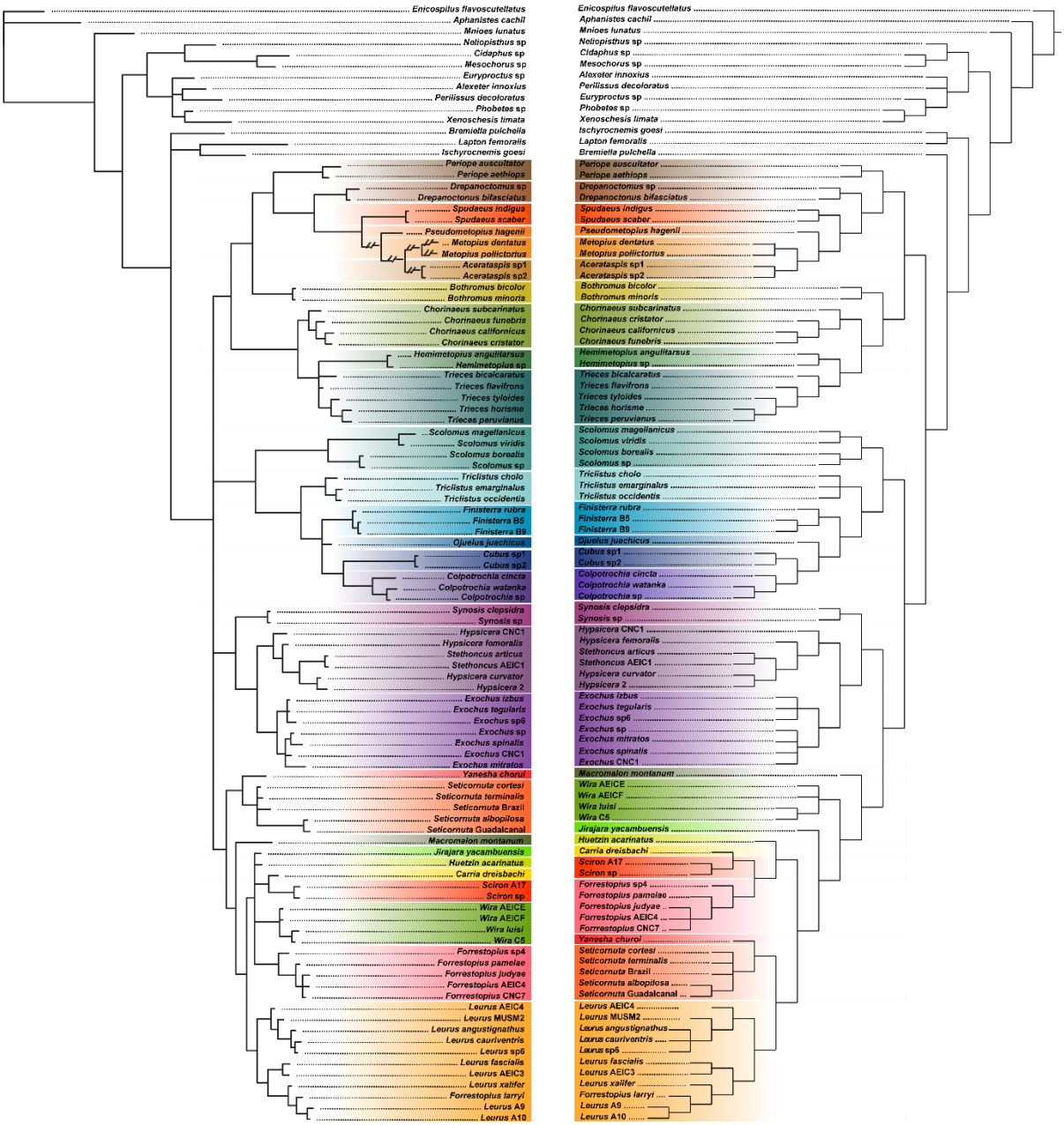

Figure 10. The strict consensus tree from parsimony analysis at the left and Bayesian analysis at the right, showing only the Metopiinae.

Monophyly of Metopiinae

The subfamily Metopiinae was recovered as monophyletic and clustered with the other Basal Ophioniformes and sister to the clade formed by Tryphoninae, Mesochorinae, and Ctenopelmatinae. Metopiinae (including *Bremiella*, *Ischyrocnemis*, *Lapton*, and *Scolomus*)

have low resampling support under the parsimony analysis (BS=12 and JS=15) and good support under Bayesian analysis (PP=0.987).

Metopiinae are supported by one unreversed synapomorphy—profemur with a concavity ventrally (100-1, but it was not coded for *Lapton*)—and three reversed synapomorphies: antennomere 2, in lateral view between 1.1–1.8× as long as wide (1-1, which is r reversed in *Scolomus*), the lower face and clypeus confluent and not separated by an impressed groove (24-1, Fig. 2A, reversed in some species of *Periope* and *Scolomus*), and dorsal posterior corner of pronotum rounded and weakly convex (57-1, Fig. 4G, reversed in *Scolomus* (Fig. 5B)), and two homoplasious character state changes: 59-1 and 63-0.

The interantennal process of the lower face with a projection between antennae (31-1; Fig. 2C) was not found as a synapomorphy, despite being one of the most conspicuous features of this subfamily, as it is lacking in *Scolomus* and *Ischyrocnemis.* Another feature that was mentioned as characteristic of Metopiinae (Gauld & Wahl 2006, Broad & Shaw 2005) is the shape of protarsomere 4, wider than long (101-1), and while it is present in most metopiines the other state – longer than wide (101-0) – is present in species of *Bremiella, Chorinaeus, Drepanoctomus, Hemimetopius, Ischyrocnemis, Lapton, Periope, Scolomus,* and *Trieces*.

Relationship among genera

Three of the currently uncertainly placed genera—*Bremiella, Ischyrocnemis,* and *Lapton*—are found basal to the remaining Metopiinae (Figs. 8, 9), while *Scolomus* was found nested well within the Metopiinae. The remaining Metopiinae (including *Scolomus*) is support by two homoplasious character state changes: occipital carina ventrally absent (40-2) and profemur more than 0.4× as wide as long (99-1, Fig. 6F); it has low resampling support under the parsimony analysis (BS=10 and JS=8) and Bayesian analysis (PP=0.665).

Aside from *Bremiella*, *Ischyrocnemis*, and *Lapton*, four main groups of genera were recovered (nominated as Clades 1–4 in Figs. 8, 9), although the relationships among them were weakly supported as characters whose transformations are fully consistent are rare. Aside from this, the topology allows us to draw some conclusions about relationships of certain genera. Each clade is discussed independently below, followed by the genera included in each clade. Most relationships among genera are similar in both analyses, except for some sister relationships obtained with the Bayesian analysis (see below).

The trees showed good support at the generic level (Figs. 8, 9), reinforcing the monophyly of several genera and several synapomorphies are proposed (see below). However, in all the analyses, *Stethoncus* was nested within *Hypsicera*; and the genus *Forrestopius* was not recovered as monophyletic, as *Forrestopius larryi* clustered with *Leurus xalifer*, *Leurus* A9, and *Leurus* A10. Additionally, five new genera were found: *Finisterra* gen. nov., *Huetzin* gen. nov., *Jirajara* gen. nov., *Wira* gen. nov., and *Yanesha* gen. nov. (see Taxonomic section).

The monophyly of *Ojuelus*, *Macromalom*, *Huetzin* gen. nov., *Jirajara* gen. nov., *Pseudometopius*, and *Yanesha* gen. nov. was not tested herein as only a single species per genus was considered for the analysis.

Clade 1

Clade 1 is justified by one reversed synapomorphy, metasomal tergite II with a pair lateromedian carinae (124-1, Fig. 6B), and three homoplasious character-state changes: 49-1 (Fig. 4H), 53-1 (Fig. 5A), and 82-1. There are some discrepancies between the results of the different analyses (Fig. 10). *Bothromus* was recovered as sister to the clade formed by *Chorinaeus*, *Hemimetopius*, and *Trieces* in the parsimony analysis with low support (BS=9 and JS=11), while under Bayesian analysis it was recovered as sister to the clade formed by

Periope, Drepanoctomus, Spudaeus, Pseudometopius, Metopius, and *Aceraspis* also with low support (PP=0.533).

Townes & Townes (1959) suggested that *Pseudometopius, Aceraspis, Chorinaeus, Hemimetopius*, and *Trieces* were related, based on the absence of laterotergites of the metasomal segments III–V. This group was subsequently subdivided in two subgroups. One of these subgroups was formed by *Chorinaeus, Hemimetopius*, and *Trieces*, which was also recovered by Quicke *et al.* (2009) with the following relationships: (*Trieces* + *Chorinaeus*) + *Hemimetopius.* In this study, with parsimony analysis the following relationship was found: *Chorinaeus* + (*Hemimetopius* + *Trieces*) and with good support (BS= 77, JS=82); while under Bayesian analysis this clade had high support (PP=1) but *Chorinaeus* was sister to a *Hemimetopius* and *Trieces*, but in this case *Trieces* was found paraphyletic with respect to *Hemimetopius.* The clade formed by *Hemimetopius* and *Trieces* was supported by two unreversed synapomorphies: mesopleural suture not discernible (70-1, Fig. 5H), and metapleuron without a sulcus dividing it, so seeming flat (74-1, Fig. 5H). These two character-state changes were suggested to be present only in *Trieces* (Gauld & Sithole 2002), but they are also present in *Hemimetopius.*

The other subgroup formed by *Aceraspis* and *Pseudometopius* (Townes & Townes 1959) was partially recovered in this study. *Pseudometopius* is found as sister to the clade formed by *Aceraspis* and *Metopius.* The sister-group relationship between *Metopius* and *Aceraspis*, was already suggested by Quicke *et al*. (2009); and it was supported by one synapomorphy, mesoscutellum with lateral ridges produced posteriorly into sharp processes that are folded distally (65-1, Fig. 5B), and five homoplasious character-state changes: 64-1, 70-1, 95-0, 96-0, 97-0, and 165-1. It is the first time that a close relationship of *Periope, Drepanoctomus, Spudaeus, Pseudometopius, Metopius*, and *Aceraspis* is supported.

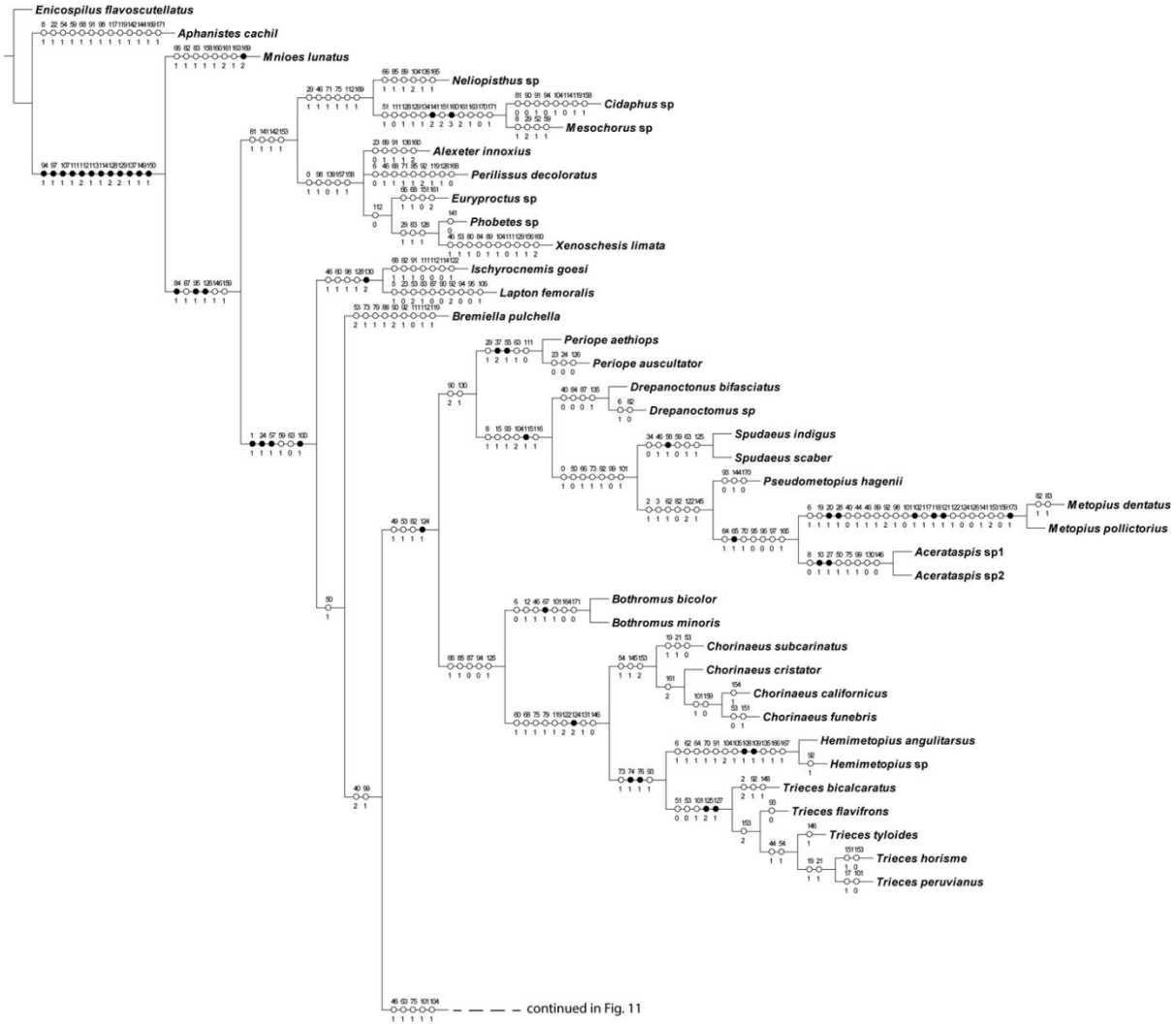

Figure 11. Tree with all character state changes mapped upon it. Black circles indicate unique character state changes; white circles indicate homoplastic changes; the changed character state is shown below.

Aceraspis Uchida 1934

The monophyly of *Aceraspis* is supported by three unreversed synapomorphies: mandible with condylar ridge interrupted and turned upwards (10-1, Fig. 2E), clypeus preapically with a transverse ridge parallel with the margin (27-1, Fig. 2E), and male with one mesotibial spur and female with two mesotibial spurs (103-2); the first two synapomorphies are newly described for the genus. It is also supported by six homoplasious character-state changes: 8-0, 50-1, 75-1, 99-1, 130-0, and 146-0. It has high support in both analyses (BS=99, JS=99, PP=1).

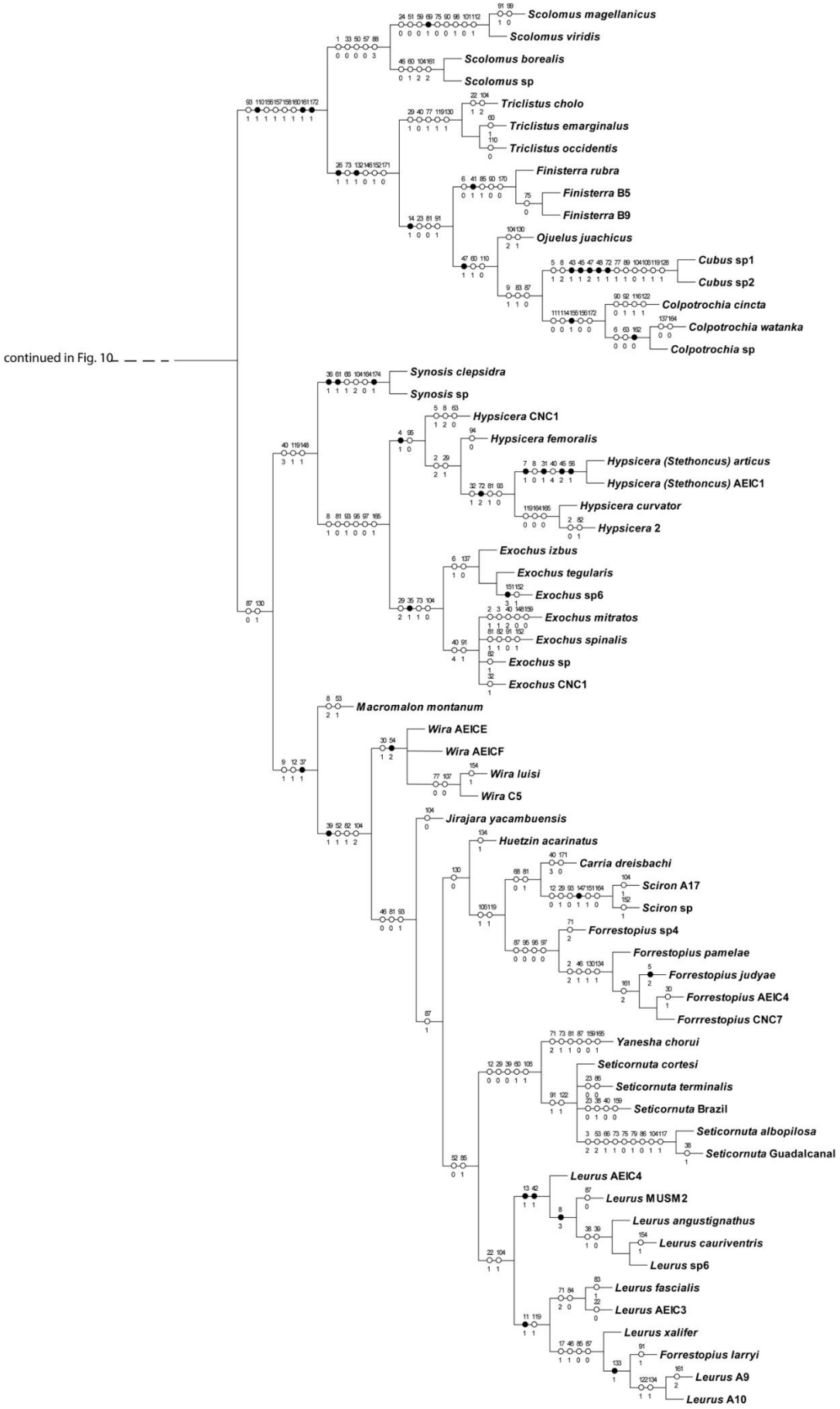

Figure 12. Continuing Fig. 11

This is a small genus that includes seven species; the species are distributed in the Eastern Palearctic, Oriental, and Australasian regions (Yu *et al*. 2012).

***Bothromus* Townes & Townes 1959**

The monophyly of *Bothromus* is supported by one unreversed synapomorphy: subalar prominence with an appearance of being folded over (67-1, Fig. 5G, this synapomorphy was proposed by Townes & Townes (1959)) and six homoplasious character-state changes: 6-0, 12-1, 46-1, 101-1, 164-0, and 171-0. It has high support (BS=99, JS=99, PP=1). *Bothromus* was found nested within the Clade 1, its sister relationship remains unclear.

This is a small, Nearctic genus that includes four species (Walley 1966).

***Chorinaeus* Holmgren 1856**

The monophyly of *Chorinaeus* is supported by three homoplasious character-state changes: 54-1, 145-1, and 153-2. The monophyly of *Chorinaeus* was questioned by Gauld & Sithole (2002); the only putative autapomorphy for *Chorinaeus* was the upper edge of pronotum paralleled by a broad, shallow submarginal groove which is discernible (54-1, Fig. 5D). Even though no unique synapomorphy was found for the genus it was recovered as monophyletic in all analyses and with high support (BS=89, JS=94, PP=0.886).

Chorinaeus is a large genus that includes 45 species (Choi *et al*. 2017); most of is diversity occurs in the Holarctic region and the mountainous areas on the Palearctic/Oriental interface (Gauld & Sithole 2002). There are two species in the Neotropical region (Gauld & Sithole 2002, pers. obs.)

***Drepanoctomus* Pfankuch 1911**

The monophyly of *Drepanoctomus* is supported by four homoplasious character-state changes: 40-0, 84-0, 87-0, and 135-1. It has high support (BS=70, JS=75, PP=0.994). This genus was analysed only based on its external morphology, and characters from the terminalia were not accessible (Table S1).

This is not very speciose genus that includes six species; the species are distributed in the Afrotropical, Australasian, Palearctic, and Oriental regions (Yu *et al*. 2012).

***Hemimetopius* Benoit 1955**

The monophyly of *Hemimetopius* is supported by two unreversed synapomorphies: metatibia, laterally, with a folding longitudinally (108-1, Fig. 6D) and metabasitarsomere laterally with a folding longitudinally (109-1, Fig. 6D); and 10 homoplasious character-state changes: 6-1, 62-1, 64-1, 70-1, 91-1, 104-2, 105-1, 135-1, 166-1, and 167-1. It has high resampling support under the parsimony analysis (BS=99 and JS=100) and good support under Bayesian analysis (PP=1).

This is not very speciose, Afrotropical, genus that includes tree species (Benoit 1955b, per. obs.).

***Metopius* Panzer 1806**

The monophyly of *Metopius* is supported by six unreversed synapomorphies: maxillary palpomere 2 of male more or less flattened anteroventrally (20-1), a facial shield (28-1), apex of mesotibia with dentiform process (102-1), male and female with one mesotibial spur (103-1), metasomal tergite I and II fused (118-1), metasomal tergite II much shorter than third tergite (121-1), and metasomal tergite VIII, dorsolaterally folded and separated by a crease (173-1); 20 homoplasious character-state changes: 8-1, 19-1, 40-0, 44-

1, 46-1, 88-1, 89-1, 92-2, 95-0, 96-0, 97-0, 98-1, 101-0, 117-1, 122-1, 124-0, 126-0, 141-1, 153-2, and 159-0.

The monophyly of *Metopius* was never questioned but its position among metopiines was one of the most uncertain. Townes & Townes (1959) suggested that the genus was "isolated" in the subfamily, while Gauld & Sithole (2002) suggested that it may be a "more specialized" member of the clade formed by *Colpotrochia*, *Cubus*, and *Triclistus*, as they share the character-state 34-1 (interantennal process reaching the frons, Fig. 3D). The position of *Metopius* is referenced above, and its placement within the subfamily was challenging historically likely as a result of it having several autapomorphies, more so than most other genera.

This is a large, cosmopolitan genus that includes 145 species (Gauld & Sithole 2002, Choi *et al*. 2015b).

***Periope* Haliday 1938**

The monophyly of *Periope* is supported by two unreversed synapomorphies: frons with a ridge surrounding the toruli that meets with the projection that extends to the frons (37-2, Fig. 3F), and pronotum with upper-anterior part with a folded section (55-1, Fig. 4I), and three homoplasious character-state changes: 29-1, 63-1, and 111-0. It has high resampling support under parsimony analysis (BS=90 and JS=94) and good support under Bayesian analysis (PP=1). A character-state that needs to be further exploration is the paramere dorsally fused (140-1), this character was not found as a synapomophy as it is also present in *Enicospilus flavoscutellatus* (the outgroup used to root the tree), or as homoplasious, coded also for *Periope aethips*.

This is not very speciose, Palaearctic, genus that includes five species (Yu *et al*. 2012).

***Spudaeus* Gistel 1848**

The monophyly of *Spudaeus* is supported by one unreversed synapomorphy: dorsal posterior corner of pronotum with a longitudinal concavity (58-1, Fig. 5C), and five homoplasious character-state changes: 34-0, 46-1, 59-0, 63-1, and 125-1. It has high resampling support under the parsimony analysis (BS=98 and JS=99) and good support under Bayesian analysis (PP=1).

This is not very speciose, Holarctic, genus that includes eight species (Yu *et al*. 2012).

***Trieces* Townes 1946**

The monophyly of *Trieces* is supported by two unreversed synapomorphies: metasomal tergite II with lateral longitudinal carinae extending entire length of tergite (125-2) and metasomal tergite III with lateral longitudinal carinae at least on anterior 0.3× of tergite length (127-1); and three homoplasious character-state changes: 51-0 (Fig. 4H), 53-0, and 101-1. It has low resampling support under the parsimony analysis (BS=31 and JS=30) and no support under the Bayesian analysis. The character-state change: 51-0 was not found as a synapomorphy for the genus because it is also present in two other genera within Metopiinae (*Lapton* and *Scolomus*) and most of the outgroups; but within the clade formed by *Chorinaeus, Hemimetopius*, and *Trieces* this feature can be useful to distinguished it from them.

This is a large genus that includes 69 species (Mazón & Bordera 2016), it has cosmopolitan but most of its diversity in northern temperate habits and few in the Southern Hemisphere (Gauld & Sithole 2002).

Clade 2

Clade 2 is supported by three reversed synapomorphies: hooked lobe on the inner surface of the distal metatarsomeres of the female (110-1, Fig. 6G), sternite VI distally ploughshare-shaped but laterally concave (161-1), and metasomal tergite VIII compressed dorsaventrally (172-1); and five homoplasious character-state changes: 93-1, 156-1, 157-1, 158-1, and 160-1. It has low resampling support under the parsimony analysis (BS=9 and JS=7) and good support under Bayesian analysis (PP=0.577).

Sister and basal to the other member of this clade is *Scolomus;* its position within Metopiinae has been subject to question; in previous analyses *Scolomus* was recovered as the sister group to the Metopiinae based on morphological and molecular data (Quicke *et al.* 2009), and subsequently considered a member of the ctenopelmatine, tribe Pionini (Yu *et al.* 2012). In this study, it is cluster within Metopiinae and among the more basal members of the subfamily (Figs. 8, 9), as previously suggested by Gauld & Wahl (2006). Gauld & Wahl (2006) placed *Scolomus* within Metopiinae based on the structure of the lower face and clypeus, weakly separated by an impressed groove, and that *S. borealis* Townes was found as parasitoid of Lepidoptera like other metopiines Broad & Shaw (2005), while the ctenopelmatines are parasitoids of hymenopteran Symphyta (Gauld & Wahl 2006).

The clade formed by *Colpotrochia*, *Cubus*, and *Triclistus* was recognized as a natural group Townes & Townes (1959), based on the interantennal process of lower face dorsally projected between antennae and reaching to the frons (34-1, Fig. 3D); similar relationship was found by Quicke *et al.* (2009). Subsequently, the genus *Ojuelus* was described and suggested to also be member of this clade (Khalaim *et al.* 2012). This study corroborates the monophyly of this clade and includes *Finisterra* gen. nov. (see Taxonomy section). This clade is justified by two unreversed synapomorphies: the presence of a sulcus from the anterior margin of the clypeus and the presence of setae only on distal margin (26-1, Fig.

2G), and distal margin of tergite VI with setae only on distal margin (132-1) and four homoplasious character-state changes: 73-1, 146-0, 152-1, and 171-0. In both analysis the clade was also found with a good support (BS=64, JS=74, PP=0.968) but the relation within have some discrepancies between the two analyses (Fig. 10). Under the parsimony analysis the following relationship was found *Triclistus* + (*Finisterra* + (*Ojuelus* + (*Cubus* + *Colpotrochia*))), while under the Bayesian analysis *Triclistus* was also found sister to the other genera, but the remaining are paraphyletic, but genera *Cubus* and *Colpotrochia* asre also found as sisters (this sister relationship was recovered in both analyses).

***Colpotrochia* Holmgren 1858**

The monophyly of *Colpotrochia* is supported by one unreversed synapomorphies: 155-1 apodeme of aedaegus longer than aedeagus (Fig. 7D), and by four homoplasious character-state changes: 111-0, 114-0, 156-0, and 172-0. It has good support under both analyses (BS=79, JS=88, PP=0.998). The monophyly of *Colpotrochia* was questioned by Gauld & Sithole (2002), as they suspected that was paraphyletic with respect to *Cubus*; as both genera are aposematic and metasoma anteriorly rather petiolate; in this study *Colpotrochia* was found monophyletic and sister to *Cubus*.

This is a large genus that includes 68 species, it is widely distributed but apparently absent in the Afrotropical region (Gauld & Sithole 2002).

***Cubus* Townes & Townes 1959**

The monophyly of *Cubus* is supported by five unreversed synapomorphies: hypostomal carina with mid ventral line (43-1, Fig. 4A), propleuron almost cubical in profile (45-1, Fig. 4D), pronotal epomia produced dorsally joining and forming a flange (47-2, Fig. 4D), pronotum without a shallow groove paralleling the anterior margin of the pronotum (48-

1, Fig. 4D), and posterior transverse carina of mesosternum, centrally with a pair of flattened finger-like processes (72-1); and by five homoplasious character-state changes: 5-1, 8-2, 77-1, 89-1, 104-0, 106-1, and 119-1. It has a high support (BS=100, JS=100, PP=1).

This is not very speciose, Neotropical, genus currently with only one describe specie but several are undescribed throughout tropical America (Gauld & Sithole 2002, per. Obs.).

***Finisterra* gen. nov.**

The monophyly of *Finisterra* is supported by one unreversed synapomophy: occipital carina when ventrally absent turned inwards (41-1, Fig. 3K) and four homoplasious character-state changes: 6-0, 85-1, 90-0, and 170-0. It has a high support (BS=96, JS=96, PP=1). This genus is described and discuss on the Taxonomic section.

This is not very speciose genus, beside the species described below, includes nine more species. It is distributed in central and south Chile, and west Argentina.

***Scolomus* Townes & Townes 1950**

Scolomus was found as a monophyletic clade. It is supported by five homoplasious character-state changes: 1-0, 33-0, 50-0, 57-0, and 88-3. It has low resampling support under the parsimony analysis (BS=0 and JS=4) and good support under Bayesian analysis (PP=0.979).

There are two clades within *Scolomus*, both with high support. The clade formed by *S. megallanicus* and *S. viridis* (BS= 90, JS=92, PP=1) which, among other features, have the clypeus and lower face separated by a groove (24-0, Fig. 2A), and the unreversed synapomorphy, subalar prominence with a sharp out-curving spine (69-1, Fig. 5B); while the other clade from by *S. borealis* and *Scolomus* sp. (BS= 84, JS=84, PP=0.917) have the

clypeus and lower face confluent and not separated by an impressed groove (24-1), and the subalar prominence not modified.

This is not very speciose, widely distributed genus, currently including six species (Araujo *et al*. 2018), and many undescribed species can be found in temperate, mountainous areas of the Neotropical region (per. obs.).

***Triclistus* Förster 1869**

Triclistus was found as a monophyletic clade; it is supported by five homoplasious character-state changes: 29-1, 40-0, 77-1, 119-1, and 130-1. It has a high resampling support under the parsimony analysis (BS=69 and JS=77) and good support under Bayesian analysis (PP=0.959). The presence of hooked lobe on the inner side of the distal metatarsomeres of female (110-1, Fig. 6G) was considered by Gauld & Sithole (2002) an apomorphy for the genus, but this structure is also present in *Finisterra* and *Scolomus.*

This is a moderately large genus comprising 94 describe species (Alvarado & Rodriguez-Berrio 2013b, Sääksjärvi & Bordera 2015, Sheng *et al*. 2013), mainly from Palaearctic and Neotropical regions (Gauld & Sithole 2002)

Clade 3

They exhibited the following relationship: *Synosis* + (*Hypsicera* + *Exochus*). This clade is justified by four homoplasies: 40-3, 119-1, and 148-1 (Fig. 12). It has low resampling support under the parsimony analysis (BS=14 and JS=17) and good support under Bayesian analysis (PP=0.862). In this study, *Exochus* was found as sister to *Hypsicera*, and *Stethoncus* was nested within *Hypsicera* (see Taxonomy section).

The close relationship between *Exochus*, *Hypsicera*, and *Stethoncus* was suggested before (Gauld & Sithole 2002, and partially by Quicke *et al.* 2009), the close relation with

Synosis was never suggest. Even more, Gauld and Sithole (2002) suggested that *Synosis* was sister to *Forrestopius,* as both have outer mid-tibial spurs longer than inner on the state (102-2, but this character-state occurs in several genera of Metopinae) and the size of the interantennal process of the lower face, which is small in *Forrestopius* (Fig. 3C) but never softly concave as in *Synosis* (Fig. 2B).

***Exochus* Gravenhorst 1829**

The monophyly of *Exochus* is supported by one unreversed synapomophy: interantennal process of lower face projected when only between antennae, in dorsal view has a with a carina-like projection surpassing the toruli (35-1, Fig. 3G) and three homoplasious character-state changes: 29-2, 73-1, and 104-0. It has low resampling support under the parsimony analysis (BS=48 and JS=55) and high support under Bayesian analysis (PP=0.979). *Exochus* is monophyletic and sister to *Hypsicera.*

Exochus is the largest metopiine genus, for which 12 species-groups were proposed (Townes & Townes 1959), but their monophyly have never tested. There is evidence to support the monophyly of the *albiceps* species-group. In this study three species were included (*E. izbus* Gauld & Sithole, *E. tegularis* and *Exochus* sp6). This clade is support by two homoplasious character-state changes: 6-1 and 137-0. It has high resampling support under both analyses (BS=70, JS=79, PP=0.966). The monophyly of the other species-groups was not tested as many more species would need to be included, and this goes beyond the scope of this study.

This is the largest genus in the subfamily, comprising about 290 species (Choi *et al.* 2016). It is cosmopolitan, with the majority of described species known from the Northern Hemisphere (Townes & Townes 1959, Gauld & Sithole 2002), and numerous undescribed species in the tropical regions (Gauld & Sithole 2002, pers. obs.).

***Hypsicera* Latreille 1829**

The monophyly of *Hypsicera* is supported by one unreversed synapomophy: female with antennomere 3 subcylindrical and compressed (4-1) and one homoplasious character-state change: 93-0. It has low resampling support under the parsimony analysis (BS=46 and JS=52) and good support under Bayesian analysis (PP=0.985).

As suggested by Gauld and Sithole (2002), *Stethoncus* presents derived features of *Hypsicera,* and should be considered a subgenus of *Hypsicera*. This clade present four unreversed synapomorphies: lower mandibular tooth turned upwards (7-1, Fig. 3A), interantennal process of lower face in front of antennae separated from lower face by prominent transverse carina (31-1, Fig. 3B), propleuron almost subspherical (45-2, Fig. 4E), and pronotum with upper part inflated, so in dorsal view the pronotal lobe rapper as large triangular structures (56-1, Fig. 4E), and two homoplasious character-state changes: 8-0 and 40-4. It has a high support with both analyses (BS=99, JS=99, PP=1).

This is a moderately large, cosmopolitan, genus comprising 69 describe species (Kang *et al*. 2016), including the five species previously in *Hypsicera* (Yu *et al*. 2012).

***Synosis* Townes & Townes 1959**

The monophyly of *Synosis* is supported by three unreversed synapomorphies: interantennal process of lower face projected interrupted, more or less concave (36-1, Fig. 2B), mesoscutum antero-laterally, next to pronotum with a concavity along the margin (61-1) and metasomal tergite VIII, of female, dorsally with a concavity (174-1), and three homoplasious character-state changes: 66-1, 104-2, and 164-0. It has a high resampling support under the parsimony analysis (BS=97 and JS=99) and good support under Bayesian analysis (PP=1). Alvarado & Rodriguez-Berrio (2013a) proposed that the character-state

metapleuron with a band of setae along the upper margin (78-1, Fig. 4G) was a potential synapomorphy for the genus but this character-state is also present in *Hypsicera.*

This genus includes 18 described species (Alvarado & Rodriguez-Berrio 2013a; Herrera *et al*. 2011a). The bulk of its diversity is in Palearctic and Neotropical regions; a single species and type of the genus, *Synosis clepsydra* Townes 1965, is distributed in the Nearctic region.

Clade 4

The clade 2 is justified by one reversed synapomorphies: frons with a ridge surrounding the toruli (37-1, Fig. 3C) and two homoplasious character-state changes: 9-1 and 12-1. It has low resampling support under the parsimony analysis (BS=7 and JS=7) and high support under Bayesian analysis (PP=0.989). The relationship among the genera show some discrepancies between the analyses (Fig. 10), with the exception that in both analyses the sister relationship between *Yanesha* and *Seticornuta,* and *Carria* with *Sciron* were recovered. Most of the nodes have low support under the parsimony analysis (although the support for each genus is high); they have a better support under Bayesian analysis but are less resolve, as *Forrestopius, Jirajara, Huetzin, Wira* and (*Carria* + *Sciron*) form a paraphyly.

Leurus was found as sister to *Seticornuta* in the study of Quicke *et al. (*2009); in this study *Leurus* is found sister to the clade formed by *Yanesha* and *Seticornuta* only under the parsimony analysis. With the Bayesian analysis the clade formed by *Yanesha* and *Seticornuta* is sister to the remaining members of this clade.

The majority of genera in this clade are found in the Neotropical region, with the exception of *Carria, Sciron,* and *Macromalon.* Fitton (1985) suggested *Sciron* was closest to *Carria* and *Hypsicera*. In this study *Carria* is found as sister to *Sciron* with good support (BS= 42, JS=50, PP=0.955) but not to *Hypsicera*.

***Forrestopius* Gauld & Sithole 2002**

Forrestopius larryi Gauld & Sithole 2002 was recovered within *Leurus.* The type species of *Forrestopius*, *F. judyae* Gauld & Sithole 2002 clustered with *F. pamelae* Gauld & Sithole 2002 and other three undescribed species. The monophyly of *Forrestopius* is supported by four homoplasious character-state changes: 87-0, 95-0, 96-0, and 97-1. It has low resampling support under the parsimony analysis (BS=50 and JS=64) and high support under Bayesian analysis (PP=0.991). Characters of the terminalia were not coded and the male characters of *F. pamelae* were only coded for the external morphology.

This is not very speciose, Neotropical, genus known to occur in mountainous areas from Costa Rica to Peru. It currently has four describe species (Gauld & Sithole 2002) and seven undescribed more from South America.

***Leurus* Townes 1946**

The monophyly of *Leurus* is supported by two homoplasious character-state changes: 22-1 and 104-1. It has low resampling support under the parsimony analysis (BS=13 and JS=17) and good support under Bayesian analysis (PP=0.885).

The most distinctive feature of *Leurus*, the shape of the mandible with a concavity along the ventral margin (13-1, Fig. 2J), was not found as a synapomorphies as it is only present in the clade containing the type species of the genus *L. cauriventris*. The character-state 22-1, three labial palpi, is present in all the species except for *Leurus* AEIC3. This character was miscoded by Quicke *et al.* (2009) and erroneously describe by Gauld & Sithole (2002). Even more the clade formed by *Forrestopius larryi*, *Leurus xalifer*, *Leurus* A9 and *Leurus* A10 have three palpi segments and four maxillary segments.

Leurus is a New World genus, comprised of 12 described species (Herrera *et al*. 2011b), most species seem to be restricted to tropical and subtropical parts of Central and South America and only one species, *Leurus caeruliventris* (Cresson, 1868), has been reported from southern Michigan to southern Brazil (Gauld & Sithole 2002).

***Sciron* Fitton 1984**

The monophyly of *Sciron* is supported by one unreversed synapomophy: paramere, in dorsal view, with inner margins with a concavity in semicircular shape (147-1) and five homoplasious character-state changes: 12-0, 29-1, 93-0, 151-1, and 194-0. It has a high resampling support under the parsimony analysis (BS=90 and JS=94) and high support under Bayesian analysis (PP=1). Fitton (1984) suggested *Sciron* was closest to *Carria* and *Hypsicera*. In this study *Carria* is found as sister to *Sciron* with good support (BS= 42, JS=50, PP=0.955) but not to *Hypsicera*.

This is a relatively large genus from Australian and Pacific region (Fitton 1984, Yu *et al*. 2012), but only tree species are described (Berry 1990).

***Seticornuta* Morley 1913**

The monophyly of *Seticornuta* is supported by two homoplasious character-state changes: 91-1 and 122-1. It has low resampling support under the parsimony analysis (BS=29 and JS=34) and high support under Bayesian analysis (PP=0.945).

The monophyly of *Seticornuta* was put in question by Gauld & Sithole (2002), who suggested that the New World species could be separated genus from the Indo-Australian species. The Indo-Australian species are clearly a monophyletic group with high support (BS= 99, JS=99, PP=1). The New World species do not form a monophyletic group probably because a heterogeneous array of species was included in this analysis to encompass the

variability within the genus. A potential synapomorphy for *Seticornuta* is the male hypopygium with distal end projected centrally (150-2), this character-state was not recover as a synapomorphy as of the five species examined only three included male individuals.

Seticornuta is a small genus, comprising of eight described species, two species from the Indo-Australian area and Japan (Choi *et al*. 2015a, Watanabe 2015), two from the Nearctic region and four from Neotropical region (Araujo & Penteado-Dias 2012), several new ones from South America (per. obs.).

***Wira* gen. nov.**

Monophyly of *Wira* is supported by one unreversed synapomophy: pronotum with upper margin with a deep groove next to upper margin (54-2, Fig. 4E) and one homoplasious character-state change: lower face with tentorial pit elevated respect to the face (30-1, Fig. 2J). It has a good resampling support under the parsimony analysis (BS=75 and JS=76) and high support under Bayesian analysis (PP=1). This genus was only coded for male individuals as no female is known to the genus.

This is a small Neotropical genus, inhabiting high elevation of the Andes. Beside the describe species (see Taxonomy section), tree other species are known.

Phylogenetic signal

In Table 1 shows the number of characters used, separated in three main groups, i.e., organized by tagma, gender, and terminalia of each sex. Of the 176 characters coded, 45 were from the head; this tagma has the highest value of RIc (83.3) among the tagmata (see Appendix 3). While the mesosoma and metasoma in this included similar numbers of characters, the mesosoma has the highest value of RIc (79.35). Characters from the head and

mesosoma had good coverage except for when the characters were linked to sexual dimorphism and one of the sexes was not coded (see Appendix 1).

Most of the characters were examined using external morphology, this included 136 characters, while internal morphology encompassed 40 characters, 20 for each gender (see list of morphological characters). Of the characters employed from the metasoma, only a third can be coded without dissection. As can be seen in Appendix 1, from the 90 species in the ingroup only 46 included characters of the terminalia and only 18 from the terminalia of one sex alone. This could be a reason for the low RIc for the metasoma. In the terminalia there are some promising characters that need further investigation. For example, character 138-1 (Fig. 7A), parameres in lateral view diagonal with respect to the base (forming an angle of at least 45º). This character state is only found in Metopiinae but the lack of coverage in this set of characters made it impossible to determine with confidence whether it serves as an unambiguous synapomorphy for the subfamily. Excluding the terminalia from the parsimony analysis resulted in 75 MPTs with 34 collapsed nodes in the consensus tree; while excluding character that were linked to gender (including also those in the terminalia) resulted in in 186 MPTs with 40 collapsed nodes in the consensus tree. It is clear that there is significant phylogenetic information resident within the terminalic sclerites of ichneumonoids, as exemplified here, and the traditional exclusion of such data in the study of the superfamily has perhaps hindered our understanding of the lineage. Indeed, greater emphasis should be placed in future studies on exploring the anatomy of male genitalia and other terminalic sclerites.

Table 1. Retention index (RI) per character set and quantitative descriptors of trees obtained from partitioned analysis using female and male characters. RIc = average retention index of character set followed, in parentheses, by median, standard deviation, and number of characters; % Unamb. Syn. = Percentage of unambiguous synapomorphic characters in the analysis of the full data matrix; MPT = number of most parsimonious trees; Collapsed nodes = number of nodes that collapsed in the consensus strict tree; L = tree length; CI = consistency index; RI = retention index of MPTs. Non-applicable are indicated by an en dash (–).

Character set	Number of characters	% Syn	RIc	MPT	Collapsed nodes	L	CI	RI
All character-states	176	48	86.53 (80.0, ± 22.36)	8	10	744	29	76
Prosoma	45	17	83.3 (87.5, ± 18.33)	–	–	–	–	–
Mesosoma	66	18	79.35 (78.5, ± 16.93)	–	–	–	–	–
Metasoma	65	14	69.08 (73.0, ± 27.32)	–	–	–	–	–
Both gender	122	38	80.85 (83.0, ± 18.28)	186	40	522	28	78
Female	30	5	68.62 (71.0, ± 23.07)	–	–	–	–	–
Male	24	6	64.08 (71.0, ± 32.22)	–	–	–	–	–
Without terminalia	136	46	79.83 (82.0, ± 18.72)	75	34	570	28	77
Male	20	4	60.85 (68.5, ± 33.12)	–	–	–	–	–
Female	20	3	69.9 (72.0, ± 25.06)	–	–	–	–	–

DISCUSSION

Metopiinae was recovered as monophyletic and clustered with the other Basal Ophioniformes, and sister to the clade comprising Tryphoninae, Mesochorinae, and Ctenopelmatinae. Most importantly, the subfamily was not recovered as representing a derived branch within Ctenopelmatinae, as had been suspected by some (Gauld & Wahl 2006, Quicke *et al*. 2009, Quicke 2015).

The genera *Bremiella, Ischyrocnemis,* and *Lapton,* were found as sister to the remaining Metopiinae. The placement of *Bremiella, Ischyrocnemis,* and *Lapton* remain far from resolved. Many features were not coded owing to the rarity of the species involved, so a single gender was examined, and dissections were not possible. Thus, many critical and informative features are missing for these species in the present analysis (see Appendix 1, 2). A similar limitation was also the case in the phylogenetic analysis undertaken by Quicke *et al*. (2009), as they were unable to code approximately a quarter of the morphological characters considered in their analysis for these genera. It is likely that the position of these genera will change once more individuals are discovered and can be examined.

Most discrepancies in this study were found in Clade 4, and relationships within this clade are likely to change as they had low support under both analyses (Figs. 8, 9). One of the potential reasons for the low support may be the fact that many characters could not be coded for this clade (see Appendix 1). The set of characters from the terminalia of *Forrestopius, Jirajara,* and *Huetzin* were not available, neither were the female terminalia of *Wira* or the male terminalia of *Yanesha,* as the last two genera are known only from one gender each. Another reason could be that most genera in this clade are found in the Neotropical region, and several of the genera — *Forrestopius, Huetzin, Jirajara, Wira,* and *Yanesha*— are distributed at high elevations, locations that are rarely sampled. Accordingly, the relationships among the genera may vary when more material becomes known.

The Clade 4 is supported by several informative characters present in the mandible. Such as the character-state 12-1 (mandible next to condylar ridge with a concavity along the ventral margin (Fig. 2F) can be found in most genera of this clade with a high RI (88). The character-state 9-1 (RI=97; mandible with abductor swelling next to upper corner (Fig. 2F) is also present in all the genera of this clade, but also in *Colpotrochia* and *Cubus* (members of the clade 2). Base on the features of the mandible, *Leurus* seems to be one of the most derived genera of the clade 4. It has a distinctive shape broad (8-3) with a ventral lobe that usually is apically truncate (12-1), so the lower distal corner is sharply angulated (13-1) (Gauld & Sithole, 2002). The characters-state 8-3 (mandible distally as wide in the base), the characters-state 12-1, and the characters-state 13-1 (condylar ridge with a concavity along the entire ventral margin) are only present in the clade containing the type species of the genus *L. cauriventris*. While the other two clades found in genus the lower distal corner curved (11-1, Fig. 2K). A feature that has been misinterpreted in *Leurus* is the number of palpomeres, most of the species (with the sole exception of *Leurus* AEIC3) have three labial palp segments (22-1). This character provides support to the monophyly (RI=72) for this genus. While the character-states 17-1 (RI=75) and 18-1 (RI=100), that denote the four maxillary palp segments in both genders, are presently only in one of the clades encountered within *Leurus.* These characters are informative, besides supporting the monophyly of the genus (22-1), as they suggest some major relationships within the genus. Most members of Clade 4 occur in the Neotropical region, except for *Carria, Sciron*, and *Macromalon.* The newly described genera, *Huetzin, Jirajara,* and *Wira*, are endemic of high elevation montane regions of the Andes.

Alike the Clade 4, most of the genera found in Clade 2 are endemic to the Neotropical region, except for the widely distributed and speciose genera *Colpotrochia* and *Triclistus*. *Scolomus*, the basal genus in this clade, has the bulk of its diversity in South America.

Colpotrochia has been suspected to be paraphyletic with respect with *Cubus*, as both genera are aposematic and metasoma anteriorly rather petiolate (Gauld & Sithole 2002). *Colpotrochia* and *Cubus* are sister taxa and monophyletic, and both seem to be derived members of this clade.

Conversely, most members of Clade 1 occur in the Northern Hemisphere (except for the Afrotropical genus *Hemimetopius*). The large genera, such as *Chorinaeus*, *Trieces*, and *Metopius*, are cosmopolitan with most of the described species occurring in northern temperate habitats and few records in other regions. The position of *Metopius* was one of the most doubted. Townes & Townes (1959) suggested that the genus was "isolated" within the subfamily, and Gauld & Sithole (2002) suggested that it may be a "more specialized" member of the clade formed by *Colpotrochia*, *Cubus*, and *Triclistus*, as they share character-state 34-1 (interantennal process reaching to frons, Fig. 3D). The character-state 34-1 was not recognized, before this study, to be present in the genera *Aceraspis*, *Drepanoctomus*, *Periope*, and *Pseudometopius*, which are the most closely related to *Metopius*.

The distinction among genera have been challenging in some cases. Fitton (1984) found problematical the distinction between *Colpotrochia* and *Triclistus*, based on his study of Australian fauna; Townes (1971) noticed that generic distinction among *Carria*, *Leurus*, and *Seticornuta* needed a revision when more material came to his attention; among others. Several characters have been proved no longer informative or informative in different degrees. For example, Gauld & Sithole (2002) suggested that the character-state 110-1 (hooked lobe on the inner surface of the distal metatarsomeres of the female, Fig. 6G) was an autapomorphic feature of *Triclistus*, this feature can be found in most *Triclistus* species but seems to be secondary lost in some species, like in *T. occidentalis*. The character-state (110-1) is present in several genera of the Clade 2 (except for *Colpotrochia* and *Cubus*); in fact, it

is a reversed synapomorphy of the clade with high RI (71); even more, this character provides evidence to include *Scolomus* within the Clade 2.

I suspect that when Townes (1971) noticed that generic distinction needed a revision, he referred in part to *Leurus* and *Seticornuta*. One of the most distinguishable features of *Seticornuta* is that laterotergites of metasomal segments II large (122-1). This character-state is present in all the species of *Seticornuta,* but also in several species of *Leurus* (like the Costa Rican species *L. gracius* Gauld & Sithole, *L. nostrus* Gauld & Sithole, and *L. pusillanimous* Gauld & Sithole). *Seticornuta*, as well as *Sciron*, are the only genera en in clade 4 that have the mandible, next tho the condylar ridge flat (12-1), a derivade feature within this clade.

Several set of characters have been rarely explored before to this study. The characters associated with sexual dimorphism has been poorly explored previously and they were found to be informative. For example, females of *Hypsicera* have the basal flagellomeres compressed (4-1), and this is uniquely found in this genus. Another character relater to the gender is the number of tibial spurs; *Metopius* in both gender presents a single spur (103-1) while in *Aceraspis* the male has presents one spur and the females presents two spurs (103-2), in both character-states are synapomorphies their respective genus.

Another set of characters that was found informative is the terminalia. Among the most informative, are the character found in the females metasomal tergite VIII. The tergite is compressed dorsal-ventrally (172-1) in most member of the clade 2 but seems be secondary lost in *Colpotrochia;* the presence of a concavity dorsally on the tergite (174-1) is a synapomorphy for *Synosis*; and, the tergite folded dorsolateral and separated by a crease (173-1) is a synapomorphy *Metopius.* Another section of the female terminalia that informative, especially for the clade 2 (Fig. 14C), is modified are sternites V–VII (157-1, 158-1) which highly sclerotize and the sternite VII is notched (162-1). Gauld & Sithole

(2002) suggested that these modifications helped to support and guide the rapier thin ovipositor, which may allow them to a precise oviposition.

The male genitalia were also informative, not only to the genus level but also to infer the relationship among subfamilies. The structure of the basal ring gives support to the separation between Basal and Upper Ophioniformes; the basal ring is complete (149-0, Fig. 7C) in the Upper Ophioniformes and is dorsally interrupted (149-1, Fig. 7H) in the Basal Ophioniformes, which coincidently includes the subfamilies with sessile metasomas, Metopiinae, Tryphoninae, Ctenopelmatinae, and Banchinae (Quicke 2015) that were included in this study.

The character-state 138-1 (paramere basally, in lateral view, forming an angle more than 45^{o}) is uniquely found in Metopiinae, it has a RI of 100 but was not found as a synapomorphy for the subfamily because several species could not be analysed. This character is worthwhile investigating, as currently the subfamily has a low supported under the parsimony analysis (BS=12 and JS=15 and most of its synapomorphies are reversed.

One limitation with this set of characters is that several species could not be coded, mostly because the many species are known from a single genus or are only known from small series and the permission to dissect them could not be obtained. From the 90 metopiine taxa examined only 46 were examined for both genders and 18 from a single gender, so there is considerable number of features missing.

Besides the limitation in the data coverage, morphology has proven to be a useful to infer the position of Metopiinae in relation to other subfamilies as well as the relationships among the genera included.

TAXONOMIC PART

In order to address the taxonomic implications of the resulting phylogeny, we propose the following nomenclatural changes: *Forrestopius larryi* Gauld & Sithole, 2002 to the genus *Leurus*, resulting in *Leurus larryi* (Gauld & Sithole, 2002) **comb. n.**; and those that follow:

Hypsicera Latreille, 1829

Hypsicera Latreille, 1829: 288. Type species (*Hypsicera*) sp. near *femoralis* Gravenhorst (=*femoralis* Fourcroy), by monotypy.

Metacoelus Förster, 1869: 161. Type species: *Exochus femoralis* Gravenhorst (=*femoralis* Fourcroy), by subsequent designation (Viereck, 1914: 93).

Polyclistus Förster, 1869: 161. Type species: *Exochus femoralis* Gravenhorst, by subsequent designation (Viereck, 1914: 120).

Plesioexochus Cameron, 1905: 102. Type species: *Plesioexochus rufipes* Cameron (=*femoralis* Fourcroy), by monotypy.

Stethoncus Townes *in* Townes & Townes, 1959: 167. Type species: *Stethoncus articus* Townes. **Syn. n.**

Hypsicera articus (Townes 1959) **comb. n.**

Hypsicera auberti (Gauld & Sithole, 2002) **comb. n.**

Hypsicera indicator (Aubert, 1965) **comb. n.**

Hypsicera monopicida (Broad & Shaw, 2005) **comb. n.**

Hypsicera sulcator (Aubert, 1963) **comb. n.**

Finisterra, new genus

Figures 3K, 6C, 6F, 13–14

Type species: *Finisterra rubra* new species.

Diagnosis. The genus *Finisterra* is most similar to *Colpotrochia, Cubus,* and *Ojuelus* as they share the interantennal process of the lower face dorsally projected between the antennae reaching to the frons, and the pronotum homogeneously concave without a distinctive section anteriorly. The genus *Finisterra* can be distinguish from them by having the occipital carina ventrally absent and turned inwards (Fig. 2K); additionally, the epomia small (vs. not long, sharp, reaching to almost the ventral corner of the pronotum as in *Colpotrochia* or dorsally joining and forming a flange as in *Cubus*), and the female with a hooked lobe on the inner surface of the distal metatarsomere 5 (like *Triclistus*).

Description. *Head.* Mandibles tapering towards apex, 0.4–0.5× as broad as base; bidentate, with upper tooth longer than lower tooth, lower tooth turned upwards; abductor swelling at center; upper edge with diagonal groove extending from upper corner to middle of mandible; mandible without ventral flange; condylar ridge straight, not interrupted, neither turned upwards; next to condylar ridge flat; labrum exposed when mandible closed; palpal formula 5:4, maxillary palpomeres slender; clypeus transverse, its apical margin straight, without preapical transverse ridge parallel to margin, with sulcus upwards from base of mandible; face+clypeus moderately convex (tentorial pit not elevated respect to face); malar space with similar texture as clypeus; upper part of face produced upwards between bases of antennae, dorsally produced into lamella reaching to median ocellus; compound eye surface bearing fine setae only in males; frons without carina surrounding toruli; integument next to toruli without striations; occipital carina ventrally absent, carina ventrally curved inwards; postgenal bridge not projected.

Mesosoma. Pronotum polished with band of setae along upper margin, with longitudinal concavity parallel to anterior margin; upper edge with shallow submarginal groove; with pocket-like structure in lower corner; pocket smooth or with striae between pocket and spiracle; epomia close to and parallel with anterior margin of pronotum. Propleurae not

swollen. Mesoscutum rather flat, with notauli impressed anteriorly; without concavity next to lateral margin; scutoscutellar groove broad, more or less smooth; mesoscutellum tapering towards distal end, with lateral carinae only reaching over prescutellar ridge. Mesopleuron moderately swollen; without sternaulus; epicnemial carina complete, laterally convergent with anterior margin of pleuron until near upper end, where it turns backwards to reach subalar prominence; subalar prominence flattened (not forming carina-like projection or horn); mesopleural suture discernible, smooth bellow speculum; posterior transverse carina presents laterally and centrally (absent in front of coxae). Metapleuron weakly convex, polished homogeneously cover by setae; ventrally with weak submetapleural carina which expand into lobe on anterior half. Propodeum with lateral longitudinal carinae complete and strong; lateromedian longitudinal carinae straight present anteriorly or reaching back to posterior transverse carina, absent or faint between posterior transverse carina and margin of propodeal insertion; anterior transverse carina absent or present (absent between lateromedian longitudinal carinae); posterior transverse carina complete, in some species faint at middle; propodeal spiracle elongate. Pro- and mesotrochantellus not differentiated; tibiae distally without dentiform process; protibial spur antero-dorsally with comb and postero-dorsally with velum; protarsomeres 2–3 slightly longer than wide, protarsomere 4 generally wider than long; pretarsal claws simple; mesotibia with two spurs of equal length; metatibia with inner margin apically with comb curved; metatibia with two spurs, outer one shorter than inner; metatarsomere 5 with hooked lobe on inner surface of distal metatarsomeres of female. Forewing with enclosed areolet, petiolate above, 1cu-a far distal to base of Rs&M; 2m-cu with one bulla. Hind wing with distal abscissa of Cu1 joining cu-a closer to 1A than to M.

Metasoma. Tergite I with lateral and lateromedian longitudinal carinae well developed, spiracle 0.3–0.4× of way along tergum; sternum I short, ending anterior to spiracle; laterotergite II 0.2–0.3× as wide as long; laterotergite III broad, 0.5–0.7× as wide as long;

laterotergites of metasomal segments III and IV separated by crease; metasomal tergite VI–VIII with setae on distal margin; metasomal tergite VIII of female flat (not folded ventrally, neither partly separated by crease; without hole), dorso-ventrally compressed; female with sterna IV–VI homogeneously sclerotized; sternum VI wider than long, female with sternum VI basally weakly concave, distally ploughshare-shaped, laterally concave and mid-posteriorly notched; male with metasomal tergites VIII+IX medially divided; male with sternum VIII wider than long with lateral margins converging distally.

Comments. The genus contains the genotype described below, and eight undescribed species from Argentina and Chile.

Distribution. This genus is distributed in central and southern Chile, and central-west Argentina, between 33º and 50º latitude South, from sea level up to 1,750m.

Etymology: The generic name *Finisterra*, derived from the Latin *Finis Terrae* in reference to the distribution of the genus, western-southern South America. The gender of the name is feminine.

***Finisterra rubra* new species**

Figures 13–14

Diagnosis. This is the only species with the combination of characters: propodeum with anterior transverse carinae present between lateral and lateromedian longitudinal carinae; propodeum (vs. black), mesofemur (vs. black, green or cream-colored), metapleuron (vs. black), and metasoma ferruginous (vs. predominantly green or cream-colored).

Description. Female: Forewing length 10 mm.

Head. Mandibles with upper tooth slightly stouter than lower tooth; malar space 0.7× as long as basal mandibular width; clypeus apical edge straight, laterally slightly convex; lower face+clypeus 1.1× as long as wide, granulate with punctures separated by 0.5–1.0× puncture

width; lateral ocellus separated from compound eye by 1.0× ocellar diameter; distance between ocelli 1.3× its own maximum diameter; gena 1.3× as long as compound eyes in lateral view; antenna with 64 flagellomeres, second flagellomere 1.3× as long as centrally broad, subapical flagellomere 1.1× as long as centrally broad, clearly longer than broad.

Mesosoma. Mesosoma generally smooth, polished and punctate; pronotum without wrinkle near pocket; mesoscutum with notaulus extending 0.2× length of mesoscutum, weak; mesoscutellum flat; metapleuron polished with isolated setae; submetapleural carina smooth, anteriorly expanded into conspicuous triangular lobe. Propodeum with lateromedian longitudinal carina strong, reaching to posterior transverse carina; posterior transverse carina complete; propodeal spiracle about 0.7× as long as distance between these carinae. Hind wing with distal abscissa of veins Rs, M, Cu1 and 1A sclerotized and distinguishable until margin of wing.

Metasoma. Tergum I 1.3× as long as posteriorly broad, lateromedian carinae extending 0.5× length of tergum; tergum II 0.5× as long as posteriorly broad; laterotergite II about 0.2× as broad as long; laterotergite III progressively broader, rounded apically, about 0.7× as broad as long measured apically.

Color. Head black. Mesosoma predominantly black except propodeum and metapleuron (but antero-lower corner black) ferruginous; forelegs black except profemur dorsally and protibia ventrally yellowish, protarsomeres brownish black; mid-leg black except mesofemur ferruginous; hind leg ferruginous except metatibia and metatarsomeres black; wings uniformly dark brownish infumate. Metasoma ferruginous.

Variation. The series of female paratypes varies from the holotype in the following: forewing length 9.8–10.5 mm lower face+clypeus 1.0–1.2× as long as wide; lateral ocellus separated from compound eye by 1.0–1.3× ocellar diameter; distance between ocelli 1.2–1.3× its own maximum diameter; gena 1.2–1.7× as long as compound eyes in lateral view; antenna

with 63–70 flagellomeres; subapical flagellomere 1.1–1.5× as long as centrally broad; tergum I 1.2–1.3× as long as posteriorly broad, lateromedian carinae extending 0.5–0.6× length of tergum.

Male. Similar to female except as follows: malar space 0.6× as long as basal mandibular width; antenna with 62–68 flagellomeres; lateral ocellus separated from compound eye by 0.9–1.0× ocellar diameter; distance between ocelli 1.3–1.4× its own maximum diameter; gena 0.9–1.0× as long as compound eyes in lateral view.

Distribution. This species is distributed in central Chile, from sea level up to 650m.

Etymology: The specific epithet is taken from the Latin term *rubra*, meaning "red", in reference to the color of the propodeum and metasoma. It is a feminine noun in the genitive case.

Holotype. ♀ "CHILE: Talca 66.5 km E. San Clemente 625 m, 35º43'S, 70º50'W 5–18 Nov 1994, R. Leschen, C. Carlton # 113 ex: Fligth intercept trap" (SEMC).

Paratypes. ♀ "Los Maitenes, Santiago, CHILE 00m. 16.x1954 L.E. Peña [CNC493473]", ♀ "El Canelo, Santiago, CHILE 25-XI-1963 L.E. Peña [CNC493474]", 3♀♀ "Aculeo Santiago [Aculeo lagoon, 33°50′47″S 70°54′55″W, 350m] 3-7-xi-59 [CNC493475–CNC493477]", ♂ "El Quisco, Chile, Santiago 1-3-xi-1951 L.E. Peña [CNC493478]", 2♂♂ "Puente Alto, Stgo, CHILE X.1952 L.E. Peña [CNC493479–CNC493480]", ♂ "CHILE, Parral Fundo Malcho 16.XI.1964 [CNC493481]", and ♂ "El Canelo, Santiago, CHILE 24.xi.1954 L.E. Peña [CNC493482]" (CNC); 2♀♀ and ♂ "Preandes Region Santiago, Chile X.'78 L. Peña", ♂ "Piscicultura Pr. Aconcagua CHILE Nov.1953 L.E. Peña", and ♀ "Fundo Malcho Pr. Linares CHILE Nov. 1956 L.E. Peña" (AEIC). ♂ "Santiago Chili Fr. Claude Joseph coll." (USNM).

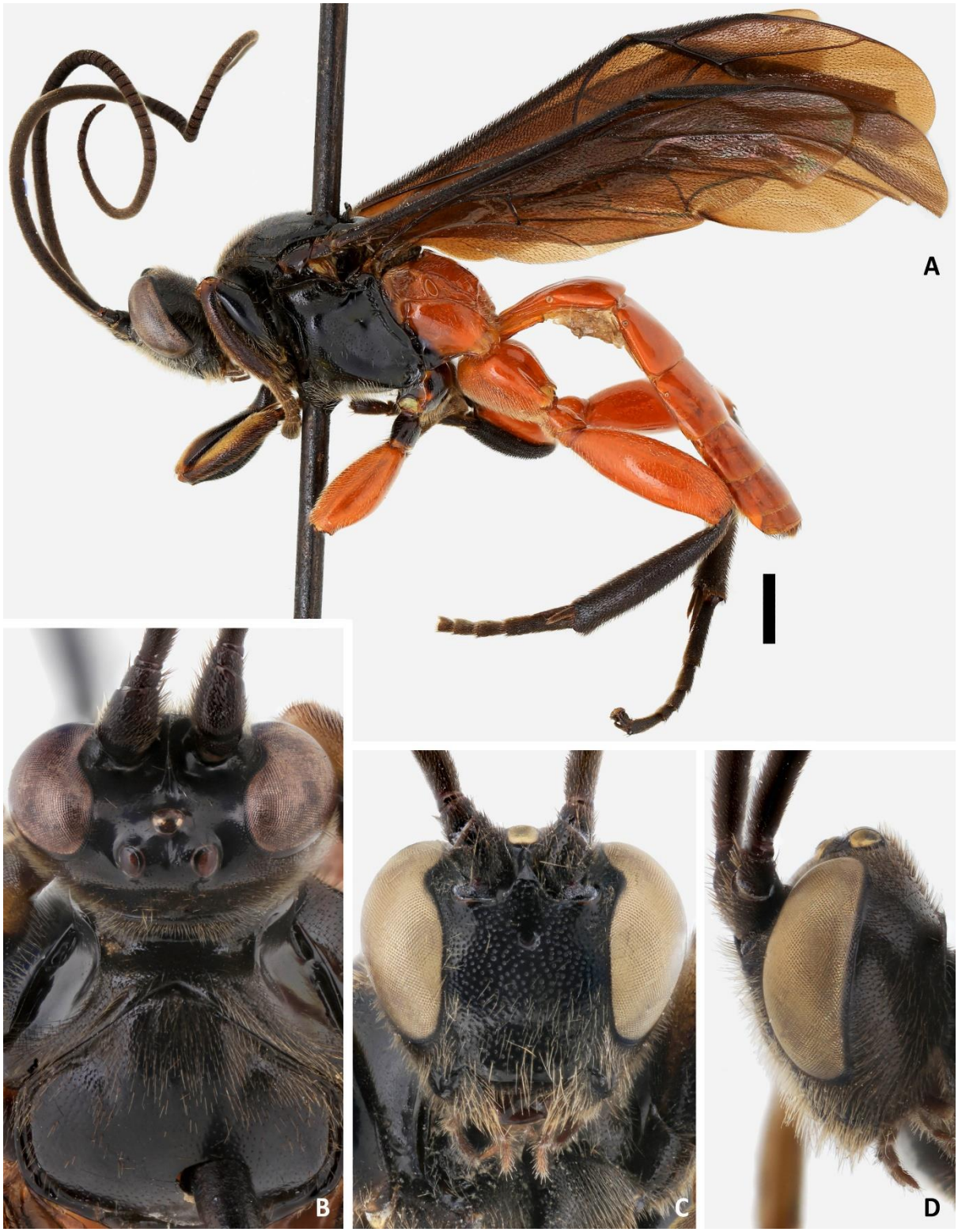

Figure 13. Morphology of *Finisterra rubra* new species **A.** Female habitus, paratype (scale bar=1mm) **B.** Head in dorsal view and mesoscutum, female holotype **C.** Head in ventral view, female holotype **D.** Head in lateral view, female holotype.

Figure 14. Morphology of *Finisterra rubra* new species. **A.** Wings, male paratype. **B.** Mesosoma in lateral view, female paratype. **C.** Distal section of metasoma in ventro-lateral view and metatarsomeres, holotype. **D.** Propodeum and first tergite of metasoma, holotype.

***Huetzin*, new genus**

Figures 15–16

Type species: *Huetzin acarinatus* new species

Diagnosis. The genus can be recognize by the following combination of characters: labrum not exposed when the mandibles are closed; palpal formula 5:4; mandible, next to condylar ridge, with a concavity along the margin (but not reaches to the distal end as in *Leurus*); upper part of the face projected into a small projection, projected upwards only between bases of the antennae; frons laterally striate with a carina surrounding the toruli; the occipital carina ventrally absent, ventrally not curved inwards; mesotibia with two spurs with the outer spur slightly longer than the inner spur; metatibia with two spurs the outer spur shorter than the inner spur; and forewing with enclosed areolet.

Description. *Head.* Mandibles tapering towards apex, 0.6–0.8× as broad as base; bidentate, with upper tooth directly below upper; abductor swelling next to upper corner; mandible with ventral flange; condylar ridge straight, not interrupted neither turned upwards; next to condylar ridge with concavity along reaching at most to 0.7 times its length; labrum not exposed when mandible closed; palpal formula 5:4, maxillary palpomeres slender; clypeus transverse, its apical margin straight; without preapical transverse ridge parallel to margin; without sulcus upwards from base of mandible; face+clypeus moderately convex (tentorial pit not elevated respect to face); groove between compound eye and mandible with distinct groove on whole length; upper part of face projected into small projection, projected upwards only between bases of antennae (this projection not reaching to median ocellus), dorsally not forming weak crest medially; frons with carina surrounding toruli, next to toruli, laterally, striate; occipital carina ventrally absent, ventrally not curved inwards; postgenal bridge not projected.

Mesosoma. Pronotum polished with band of setae along upper margin, with longitudinal concavity parallel to anterior margin; upper edge homogeneously convex; with pocket-like structure in lower corner, with wrinkle projecting upwards from pocket-like structure, below pocket-like structure with wrinkles; epomia absent. Propleurae not swollen. Mesoscutum weakly convex, with notauli impressed; without concavity next to lateral margin; scutoscutellar groove broad and smooth; mesoscutellum tapering towards distal end, with lateral carinae only reaching over prescutellar ridge. Mesopleuron moderately swollen without sternaulus; with epicnemial carina complete, converging with anterior margin of pleuron until near upper end, where it sharply turns forwards to reach margin almost at level at subalar prominence; subalar prominence convex to weakly flattened (not forming carina-like projection or horn); mesopleural suture discernible, smooth bellow speculum; posterior transverse carina presents laterally and centrally (absent in front of coxae). Metapleuron almost flat, polished, glabrous with few isolate setae; ventrally with weak submetapleural carina expanded into lobe anteriorly. Propodeum with lateral longitudinal carina absent; lateromedian longitudinal carinae present only basally; distally with small longitudinal carinae next to margin of propodeal insertion; distally, next to margin of propodeal insertion with convexity in analogous position to lateromedian longitudinal carinae; anterior and posterior transverse carinae absent; propodeal spiracle elongate. Pro- and mesotrochantellus undifferentiated; protibial spur antero-dorsally with comb and postero-dorsally with velum; protarsomeres 2–3 slightly longer than wide, protarsomere 4 generally wider than long; pretarsal claws simple; mesotibia with two spurs, outer one slightly longer than inner; metatibia with inner margin apically with comb curved; metatibia with two spurs, outer one shorter than inner; metatarsomere 5 without hooked lobe on inner side of distal metatarsomeres of female. Forewing with enclosed areolet, 1cu-a far distal to base of Rs&M;

2m-cu with one bulla. Hind wing with distal abscissa of Cu1 joining cu-a closer to 1A than to M.

Metasoma. Tergite I with lateral and lateromedian longitudinal carinae well developed, spiracle 0.3–0.4 of way along tergum; sternum I short, ending anterior to spiracle; laterotergite II 0.2× as wide as long; laterotergite III 0.4–0.5× as wide as long; laterotergites of metasomal segments III and IV separated by crease; metasomal tergites VI–VIII without setae on distal margin; male with metasomal tergites VIII+IX medially divided; paramere distally flat, in lateral view more or less diagonal.

Comments. The genus contains only the genotype described below. This genus is distributed in the high plateaus in the center of Mexico between 2900–3000m of elevation.

Etymology: The generic epithet is derived from *Huetzin*, one of the rulers a pre-Columbian Toltec culture that dominated the north of the Mexican highlands. The gender of the genus name is masculine.

***Huetzin acarinatus* new species**

Figures 15–16

Diagnosis. Similar to the genus, as it is a monotypic genus.

Description. Female: Forewing length 5.6 mm.

Head. Mandibles with upper tooth 1.5× longer than lower tooth; malar space 0.8× as long as basal mandibular width; clypeus apical edge straight; lower face+clypeus 1.0× as long as wide, granulate with punctures separated by 0.5–1.0× puncture width and softly striate; lateral ocellus separated from compound eye by 1.1× ocellar diameter; distance between ocelli 1.2× its own maximum diameter; gena 1.0× as long as compound eyes in lateral view; antenna with 27 flagellomeres, second flagellomere 1.1× as long as centrally broad, subapical flagellomere 1.0× as long as centrally broad.

Mesosoma. Mesosoma generally smooth, polished and punctate; pronotum with wrinkles bellow pocket and with wrinkle projecting upwards from pocket-like structure; mesoscutum with notaulus extending 0.2× length of mesoscutum, faint; mesoscutellum flat; metapleuron polished with isolated setae anteriorly; submetapleural carina smooth, anteriorly expanded into conspicuous triangular lobe, lobe striate. Propodeum with lateromedian longitudinal carina present only basally. Forewing with vein 2rs-m 0.5× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of veins R short, veins M, Cu1 and 1A undistinguishable.

Metasoma. Tergum I 1.5× as long as posteriorly broad, lateromedian carinae extending 0.3× length of tergum; tergum II 0.9× as long as posteriorly broad; laterotergite II about 0.2× as broad as long; laterotergite III progressively broader, rounded apically, about 0.4× as broad as long measured apically.

Color. Head and mesosoma predominantly black except palpi light brown, legs brown propodeum and metapleuron (but protibia ventrally and protarsomere and metatibia basally brownish yellow). Metasoma brown.

Variation. The series of female paratypes varies from the holotype in the following: malar space 0.8–0.9× as long as basal mandibular width; lateral ocellus separated from compound eye by 1.1–1.3× ocellar diameter; distance between ocelli 1.3–1.6× its own maximum diameter; gena 0.9–1.1× as long as compound eyes in lateral view; antenna with 25–28 flagellomeres; forewing with vein 2rs-m 0.5–0.6× as long as abscissa of M between 2rs-m and 2m-cu. Several individuals have also the head and mesosoma brown.

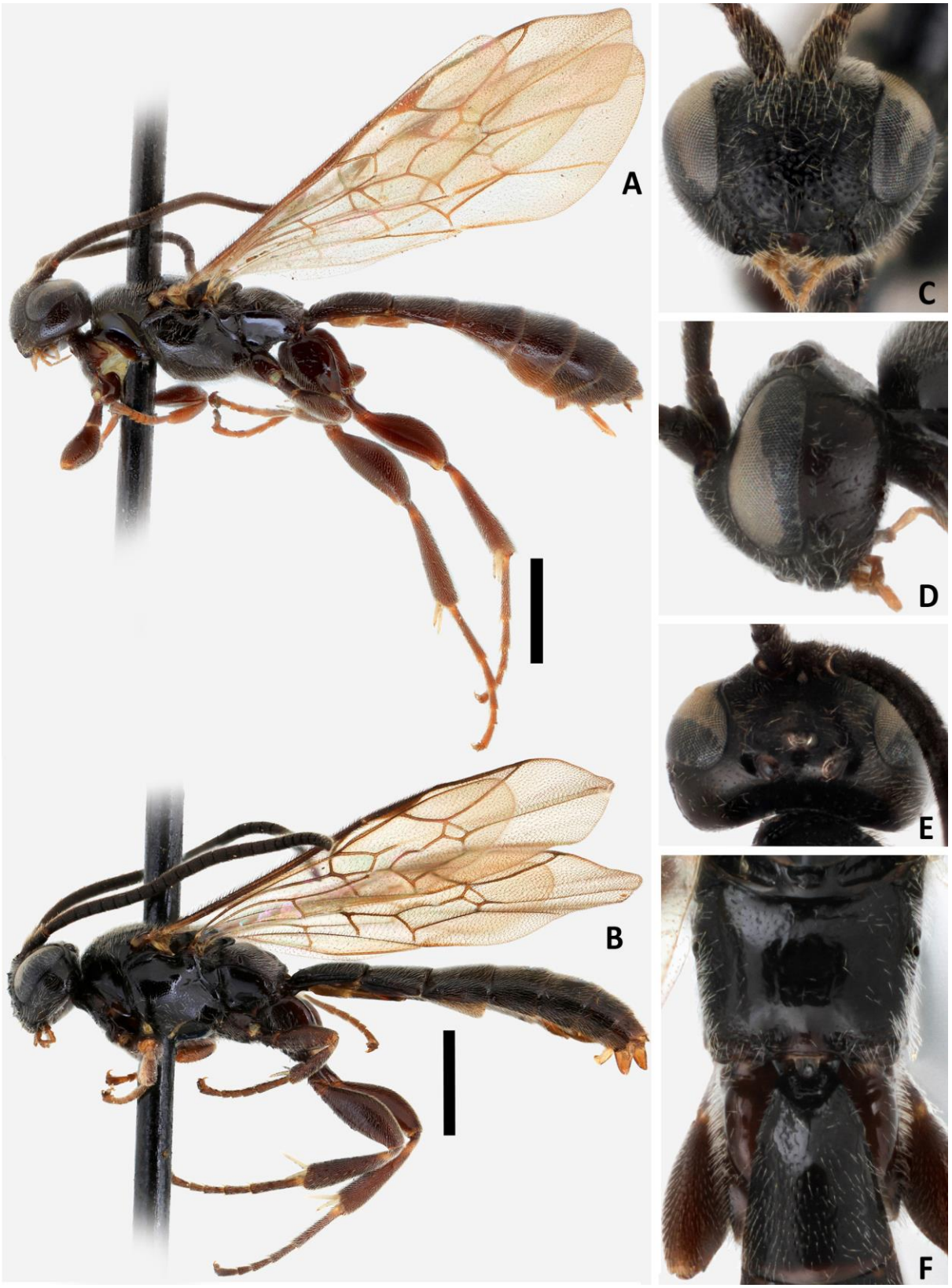

Figure 15. Morphology of *Huetzin acarinatus* new species **A.** Female habitus, holotype (scale bar=1mm). **B.** Male habitus, paratype. **C.** Head in ventral view, holotype. **D.** Head in lateral view, female paratype. **E.** Head in dorsal view, female paratype. **F.** Pronotum and first metasomal tergum, female paratype.

Figure 16. Morphology of *Huetzin acarinatus* new species **A.** Wings, female paratype. **B.** Head in lateral view and pronotum, male paratype. **C.** Mesosoma in lateral view, holotype.

Male. Similar to female except as follows: lower face+clypeus 1.0–1.1× as long as wide; malar space 1.0–1.1× as long as basal mandibular width; lateral ocellus separated from compound eye by 1.1–1.3× ocellar diameter; distance between ocelli 1.4–1.5× its own maximum diameter; gena 0.9–1.1× as long as compound eyes in lateral view; second flagellomere 1.1–1.2× as long as centrally broad; subapical flagellomere 1.0–1.1× as long as centrally broad; forewing with vein 2rs-m 0.8–1.3× as long as abscissa of M between 2rs-m and 2m-cu.

Etymology: The generic epithet *acarinatus* refers to the propodeum that lacks the majority of carinae. It is a masculine noun in the genitive case.

Holotype. ♀ "Desierto de los Leones Distrito Fed., Mexico X.13.62 2900m. H. & M. Townes" (AEIC)

Paratypes. 2♀♀, 4♂♂ same as holotype, and 3♀♀, ♂ "Hidalgo Natl. Park State of Mex., Mex. X.12.62 3000m H. & M. Townes" (AEIC); ♂ "MEXICO Desierto de Los Leones. VII-1965 NHKKrauss" (USNM).

***Jirajara*, new genus**

Figures 17–18

Type species: *Jirajara yacambuensis* new species

Diagnosis. The genus can be recognized by the combination of characters: labrum not exposed when the mandibles are closed; palpal formula 5:4; mandible, next to condylar ridge, with a concavity along the margin (but not reaches to the distal end as in *Leurus*); upper part of the face projected into a small projection, projected upwards only between bases of antennae; frons laterally striate with a carina surrounding the toruli; the occipital carina ventrally absent, ventrally not curved inwards; mesotibia with two spurs, the inner spur slightly longer than the outer spur; metatibia with two spurs, the outer spur shorter than the inner spur; and forewing with areolet open.

Description. *Head.* Mandibles tapering towards apex, 0.6–0.7× as broad as base; bidentate, with upper tooth directly below upper; abductor swelling next to upper corner; mandible with ventral flange; condylar ridge straight, not interrupted neither turned upwards; next to condylar ridge with concavity along reaching at most to 0.7×its length; labrum not exposed when mandible closed; palpal formula 5:4, maxillary palpomeres slender; clypeus transverse, its apical margin straight or weakly convex; without preapical transverse ridge parallel to

margin; without sulcus upwards from base of mandible; face+clypeus moderately convex (tentorial pit not elevated respect to face); groove between compound eye and mandible with distinct groove on whole length; upper part of face projected into small projection, projected upwards only between bases of antennae (this projection not reaching to median ocellus), dorsally not forming weak crest medially; frons with carina surrounding toruli, next to toruli, laterally, striate; occipital carina ventrally absent, ventrally not curved inwards; postgenal bridge not projected.

Mesosoma. Pronotum polished with band of setae along upper margin, with longitudinal concavity parallel to anterior margin; upper edge homogeneously convex; with pocket-like structure in lower corner, with or without wrinkle projecting upwards from pocket-like structure; below pocket-like structure smooth; epomia absent. Propleurae not swollen. Mesoscutum weakly convex, with notauli impressed; without concavity next to lateral margin; scutoscutellar groove broad and smooth; mesoscutellum tapering towards distal end, with lateral carinae only reaching over prescutellar ridge. Mesopleuron moderately swollen with small and shallow sternaulus; with epicnemial carina complete, converging with anterior margin of pleuron until near upper end, where it sharply turns forwards to reach margin almost at level at subalar prominence; subalar prominence convex to weakly flattened (not forming carina-like projection or horn); mesopleural suture discernible, smooth bellow speculum; posterior transverse carina present only laterally. Metapleuron almost flat, polished, glabrous with few isolate setae; ventrally with weak submetapleural carina expanded into lobe anteriorly. Propodeum with lateral longitudinal carina absent, lateromedian longitudinal carinae present but weak, more or less parallel to each other back to posterior transverse carina absent and converging to form single carina that joins to margin of propodeal insertion; between posterior transverse carina and margin of propodeal insertion with convexity in analogous position to lateromedian longitudinal carinae; anterior transverse

carina absent; posterior transverse carina complete, rarely absent; propodeal spiracle elongate. Pro- and mesotrochantellus undifferentiated; protibial spur antero-dorsally with comb and postero-dorsally with velum; protarsomeres 2–3 slightly longer than wide, protarsomere 4 generally wider than long; pretarsal claws simple; mesotibia with two spurs, inner one slightly longer than outer; metatibia with inner margin apically with comb curved; metatibia with two spurs, outer one shorter than inner; metatarsomere 5 without hooked lobe on inner side of distal metatarsomeres of female. Forewing with areolet open, 1cu-a far distal to base of Rs&M; 2m-cu with one bulla. Hind wing with distal abscissa of Cu1 joining cu-a closer to 1A than to M.

Metasoma. Tergite I with lateral and lateromedian longitudinal carinae well developed, spiracle 0.3–0.4 of way along tergum; sternum I short, ending anterior to spiracle; laterotergite II 0.1× as wide as long; laterotergite III 0.5× as wide as long; laterotergites of metasomal segments III and IV separated by crease; metasomal tergites VI–VIII without setae on distal margin.

Comments. The genus contains the species described below, and one undescribed species from Colombia.

Distribution. This genus is distributed from central Colombia to Venezuela, between 04º–09ºN, inhabiting the Andes mountains between 1,200–3,800m of elevation.

Etymology: The generic epithet is derived from the group of languages Jirajara which is extinct and was spoken in western Venezuela. The gender of the genus name is neuter.

***Jirajara yacambuensis* new species**

Figures 17–18

Diagnosis. *Jirajara yacambuensis* can be distinguish, from the undescribed species from Colombia, in having the tergum I 1.2× as long as posteriorly broad (vs. 1.8×), lateromedian carinae extending 0.2× length of tergum (vs. 0.4×).

Description. Female: Forewing length 4.3 mm.

Head. Mandibles with upper tooth 1.5× longer than lower tooth; malar space 1.1× as long as basal mandibular width; clypeus apical edge straight, slightly convex; lower face+clypeus 0.9× as long as wide, granulate with punctures separated by 0.5–1.3× puncture width; lateral ocellus separated from compound eye by 1.1× ocellar diameter; distance between ocelli 1.3× its own maximum diameter; gena 0.9× as long as compound eyes in lateral view; antenna with 22 flagellomeres, second flagellomere 1.2× as long as centrally broad, subapical flagellomere elongate, 1.3× as long as centrally broad, clearly longer than broad.

Mesosoma. Mesosoma generally smooth, polished and punctate; pronotum without wrinkle projecting upwards from pocket-like structure; mesoscutum with notaulus extending 0.2× length of mesoscutum, weak; mesoscutellum flat; metapleuron polished with isolated setae distally; submetapleural carina smooth, anteriorly expanded into conspicuous triangular lobe. Forewing with vein 2rs-m 0.7× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of veins M faint; veins Rs, Cu1 and 1A sclerotized only basally and distinguishable until margin of wing.

Metasoma. Tergum I 1.2× as long as posteriorly broad, lateromedian carinae faint, extending 0.2× length of tergum; tergum II 0.8× as long as posteriorly broad; laterotergite II about 0.1× as broad as long; laterotergite III progressively broader, rounded apically, about 0.5× as broad as long measured apically.

Color. Head black, with palpi pale yellowish. Mesosoma predominantly black except propodeum dark blue with metallic shines, profemur brown with distal third yellowish, protibia and protarsameres dorsally brownish and ventrally yellowish, meso- and

metatarsomeres brownish; wings hyaline, veins brown. Metasoma dark blue with tergite metallic shines, laterotergites and sternites brown.

Figure 17. Morphology of *Jirajara yacambuensis* new species (Holotype), female. **A.** Habitus (scale bar=1mm). **B.** Head in ventral view. **C.** Head in dorsal view. **D.** Mesosoma in lateral view. **E.** Pronotum and first metasomal tergum laterodorsally.

Figure 18. Morphology of *Jirajara yacambuensis* new species (paratype), male. **A.** Habitus (scale bar=1mm). **B.** Head in lateral view and pronotum. **C.** Head in dorsal view and mesoscutum.

Male. Similar to female except as follows: lower face+clypeus 0.8× as long as wide; lateral ocellus separated from compound eye by 1.3× ocellar diameter; distance between ocelli 1.7× its own maximum diameter; gena 0.9× as long as compound eyes in lateral view; antenna with 24 flagellomeres; subapical flagellomere elongate, 1.1× as long as centrally broad;

pronotum with wrinkle projecting upwards from pocket-like structure; forewing with vein 2rs-m 0.8× as long as abscissa of M between 2rs-m and 2m-cu; head with palpi pale brown.

Distribution. *Jirajara yacambuensis* was collected in the southern slope of the Portuguesa Mountain Range, on the foothills of the Andes Mountains, at 1,200m of elevation.

Holotype. ♀ "Yacambú, Venez. 1200m V.13.81 H. K. Townes" (AEIC)

Paratype. ♂ "Yacambú, Venez. 1200m V.7.81 H. K. Townes" (AEIC).

Etymology: The specific epithet is based on the type locality Yacambú.

***Wira*, new genus**

Figures 3J, 5E, 7A, 7H, 19

Type species: *Wira luisi* new species

Diagnosis. The genus can be recognize by the following combination of characters: labrum not exposed when the mandibles are closed; palpal formula 5:4; mandible, next to condylar ridge, with a concavity along the margin (but not reaches to the distal end as in *Leurus*); upper part of the face projected into a small projection, projected upwards only between bases of antennae; frons laterally striate with a carina surrounding the toruli; the occipital carina ventrally absent, ventrally not curved inwards; mesotibia with two spurs, the outer spur slightly longer than the inner spur; metatibia with two spurs, the outer spur shorter than the inner spur; and forewing with areolet open.

Description. *Head.* Mandibles tapering towards apex, 0.5–0.7× as broad as base; bidentate, with upper tooth directly below upper; abductor swelling next to upper corner; mandible with ventral flange; condylar ridge straight, not interrupted neither turned upwards; next to condylar ridge with concavity along reaching at most to 0.7× its length; labrum not exposed when mandible closed; palpal formula 5:4, maxillary palpomeres slender; clypeus slightly convex, transverse, its apical margin straight and with concavity along margin; without

preapical transverse ridge parallel to margin; without sulcus upwards from base of mandible; face+clypeus moderately convex; tentorial pit elevated respect to face; groove between compound eye and mandible with indicated as change in sculpture; upper part of face projected into small projection, projected upwards only between bases of antennae (this projection not reaching to median ocellus), dorsally not forming weak crest medially; frons with carina surrounding toruli, next to toruli, laterally, striate; occipital carina ventrally absent, ventrally not curved inwards; postgenal bridge not projected.

Mesosoma. Pronotum polished with band of setae along upper margin, with longitudinal concavity parallel to anterior margin; upper edge with shallow submarginal groove; with pocket-like structure in lower corner, with wrinkle projecting upwards from pocket-like structure, below pocket generally smooth; epomia small. Propleurae not swollen. Mesoscutum weakly convex, with notauli impressed; without concavity next to lateral margin; scutoscutellar groove broad9 and smooth; mesoscutellum tapering towards distal end, with lateral carinae only reaching over prescutellar ridge. Mesopleuron moderately swollen with small and shallow sternaulus; with epicnemial carina complete, converging with anterior margin of pleuron until near upper end, where it sharply turns forwards to reach margin almost at level at subalar prominence; subalar prominence convex to weakly flattened (not forming carina-like projection or horn); mesopleural suture discernible, smooth bellow speculum; posterior transverse carina presents laterally and centrally (absent in front of coxae). Metapleuron weakly convex, polished homogeneously cover by setae; ventrally with weak submetapleural carina which expand into lobe on anterior half. Propodeum with lateral longitudinal carina present and strong; lateromedian longitudinal carinae strong, more or less parallel to each other, between posterior transverse carina and margin of propodeal insertion absent; anterior transverse carina absent; posterior transverse carina complete; propodeal spiracle elongate. Pro- and mesotrochantellus differentiated, rarely protrochantellus distinctly

undifferentiated; protibial spur antero-dorsally with velum and postero-dorsally with comb; protarsomeres 2–3 slightly longer than wide, protarsomere 4 generally wider than long; pretarsal claws simple; mesotibia with two spurs, outer one slightly longer than inner; metatibia with inner margin apically with comb curved; metatibia with two spurs, outer one shorter than inner. Forewing with areolet open, 1cu-a far distal to base of Rs&M; 2m-cu with one bulla. Hind wing with distal abscissa of Cu1 joining cu-a closer to 1A than to M.

Metasoma. Tergite I with lateral and lateromedian longitudinal carinae well developed, spiracle 0.3–0.5× of way along tergum; sternum I short, ending anterior to spiracle; laterotergite II 0.1–0.2× as wide as long; laterotergite III broad, 0.4–0.5× as wide as long; laterotergites of metasomal segments III and IV of male separated by crease; metasomal tergites VI–VIII without setae on distal margin; male with sternum VIII wider than long, lateral margins converging distally, distal end emarginatus; paramere distally flat, in lateral view more or less diagonal; apodemes of aedeagus shorter than aedeagus.

Distribution. This genus is distributed from central Colombia to south Peru, between 05ºN and 13ºS, inhabiting the Andes mountains between 2,940–4,100m of elevation.

Etymology: The generic epithet is derived from Viracocha, the great creator deity in the pre-Inca and Inca mythology. The gender of the name is neuter.

Figure 19. Morphology of *Wira luisi* new species. **A.** Male habitus, holotype (scale bar=1mm). **B.** Head in ventral view, paratype. **C.** Head in dorsal view and mesoscutum, paratype.

Comments. The genus contains the genotype described below, and four undescribed species from Colombia and Ecuador. Most of its diversity is found in high elevation montane areas of Ecuador. All the specimens studied are males, no female is known.

***Wira luisi* new species**

Figs. 3J, 5E, 7A, 7H, 19

Diagnosis. *Wira luisi* can be distinguish from the undescribed species in having the tergum I 1.1× as long as posteriorly broad (vs. 1.4–2.3×), propodeum with combined area externa and dentipara 2.1–2.3× as long as wide (vs. 3.0–4.0×) and fore tibia pale yellow (vs. brown or black).

Description. ♂: Forewing length 7.0 mm.

Head. Mandibles weakly tapered, lower tooth shorter and slightly less broad; malar space 0.7× as long as basal mandibular width; lower face+clypeus 1.0× as long as wide; clypeus slightly convex, apically weakly convex, alutaceous with isolate punctures; face striate with isolate punctures; lateral ocellus separated from compound eye by 1.6× ocellar diameter; distance between ocelli 1.1× its own maximum diameter; gena 1.1× as long as compound eyes in lateral view; frons smooth with punctures separated by 4.0–5.0× puncture width, striate around toruli; gena and vertex smooth with punctures separated by 3.0–4.0× puncture width; antenna with 27 flagellomeres, second flagellomere 1.1× as long as centrally broad, subapical flagellomere elongate, 1.1× as long as centrally broad.

Mesosoma. Mesosoma polished; pronotum with band of setae along upper and posterior half apical margins, with several wrinkle from pocket-like structure to anterior-upper; mesoscutum alutaceous with punctures separated by 0.5–1.0× puncture width; notaulus extending 0.6× length of mesoscutum, weak; mesoscutellum slightly convex; mesopleuron smooth with punctures separated by 3.0–4.0× puncture width, with weakly impressed mesopleural suture; metapleuron polished with punctures separated by 1.0–2.0× puncture width except without setae next to submetapleural carina; submetapleural carina scrobiculate, anteriorly expanded into conspicuous triangular lobe with punctures separated by 0.5–1.0× puncture width. Propodeum with lateromedian longitudinal carina strong,

slightly closer anteriorly, absent behind posterior transverse carina; lateral longitudinal carina parallel to pleural carina; posterior transverse carina present; combined areae externa and dentipara 2.1× as long as wide (wide measured on distal margin); propodeal spiracle about 0.4× as long as distance between these carinae. Forewing with vein 2+3rs-m 1.1× as long as abscissa of M between 3rs-m and 2m-cu. Hind wing with distal abscissa of Cu1 sclerotized throughout.

Metasoma. Metasoma with tergum I 1.1× as long as posteriorly broad, lateromedian carinae extending 0.4× length of tergum, alutaceous; tergum II 1.1× as long as posteriorly broad, alutaceous; tergites III–VII alutaceous; laterotergum II inconspicuous; laterotergum III progressively broader, rounded apically, about 0.4× as broad as long measured apically.

Color. Head extensively black except mouth parts (mandible black) and scape yellow and distal 1/3 pedicel yellowish brown and basal 2/3 brown. Mesosoma black except tegula white; fore legs with coxa black, trochanter yellowish brown (laterally softly infuscate), femur yellowish brown except apically pale yellow, tibia pale yellow, and tarsomeres yellowish brown (tarsomeres 5 infuscate; mid leg with coxa, trochanter and basal half of femur black, distal half of femur and basal 2/3 of tibia whitish cream, and, distal 1/3 of tibia and tarsomeres brownish; and, hind leg with coxa, trochanter, basal 3/4 of femur black, distal 1/3 of tibia and tarsomeres black, trochantellus brownish, and, distal ¼ of femur and basal 2/3 of tibia whitish cream; metasoma black with tergite soft metallic blue reflection, and, sterna brown.

Female. Unknown

Variation. The paratype differs from the holotype in having the forewing length 7.3 mm, malar space 0.6× as long as basal mandibular width, lateral ocellus separated from compound eye by 1.5× ocellar diameter, distance between ocelli 1.0× its own maximum diameter,

subapical flagellomere 1.0× as long as centrally broad, propodeum with combined areae externa and dentipara 2.3× as long as wide, and tergum II 1.0× as long as posteriorly broad.

Distribution. This species has southernmost distribution and at the lower elevation of the genus, collected at 2,940m. It was collected in a cloud forest in the eastern slopes of the Andes.

Etymology: The specific epithet *luisi* is in honor to Peruvian entomologist Luis Figueroa. It is a masculine noun in the genitive case.

Holotype. ♂, "PERU: Cusco Dept., Wayqecha Field Station, canopy platform 13.19265ºS 71.58844ºW, 2940m 11.V.2011 DJ Bennett, hand coll. Ex. Platform, canopy vegetation PER-11-DJB-008" (MUSM).

Paratype. Same data as holotype (SEMC), genitalia dissected and preserved in a glass vial.

***Yanesha*, new genus**

Fig. 20

Type species: *Yanesha chorui* new species.

Diagnosis. The genus can be recognize by the following combination of characters: labrum not exposed when the mandibles are closed; palpal formula 5:4; mandible next to condylar ridge, flat; upper part of the face projected into a small projection, projected upwards only between bases of antennae; frons without a carina surrounding the toruli, integument next to toruli with same texture as frons; occipital carina ventrally absent, ventrally not curved inwards; mesotibia with two spurs, the outer spur slightly longer than the inner spur; metatibia with two spurs, outer spur shorter than the inner spur; and forewing with areolet open.

Figure 20. Morphology of *Yanesha chorui* new species. **A.** Female habitus (scale bar=1mm). **B.** Head in ventral view. **C.** Mesosoma in lateral view. **D.** Head in dorsal view.

Description. *Head.* Mandibles tapering towards apex, 0.6× as broad as base; bidentate, with upper tooth directly below upper; abductor swelling next to upper corner; mandible without

ventral flange; condylar ridge straight, not interrupted neither turned upwards; next to condylar ridge flat; labrum not exposed when mandible closed; palpal formula 5:4, maxillary palpomeres slender; clypeus transverse, its apical margin straight; homogeneously convex without preapical transverse ridge parallel to margin and without sulcus upwards from base of mandible; face+clypeus moderately convex (tentorial pit not elevated respect to face); malar space with similar texture as clypeus; upper part of face projected into small projection, projected upwards only between bases of antennae (this projection not reaching to median ocellus), dorsally not forming weak crest medially; frons without carina surrounding toruli, integument next to toruli with same texture as frons; occipital carina ventrally absent, ventrally not curved inwards; postgenal bridge not projected.

Mesosoma. Pronotum polished with band of setae along upper margin, with longitudinal concavity parallel to anterior margin, upper edge homogeneously convex; with pocket-like structure in lower corner, without wrinkle projecting upwards from pocket-like structure, below pocket generally smooth; epomia absent. Propleurae not swollen. Mesoscutum weakly convex, without notauli impressed, without concavity next to lateral margin; scutoscutellar groove broad and smooth; mesoscutellum tapering towards distal end, with lateral carinae only reaching over prescutellar ridge. Mesopleuron moderately swollen without sternaulus; with epicnemial carina complete, converging with anterior margin of pleuron until near upper end, where it isharply turns forwards to reach margin almost at level at subalar prominence; subalar prominence convex to weakly flattened (not forming carina-like projection or horn); mesopleural suture discernible, smooth bellow speculum; posterior transverse carina present only laterally. Metapleuron almost flat, polished, glabrous with few isolate setae; ventrally with weak submetapleural carina expanded into lobe anteriorly. Propodeum with lateral longitudinal carina present only between posterior transverse carina and margin of propodeal insertion; lateromedian longitudinal carinae strong, more or less parallel to each other,

between posterior transverse carina and margin of propodeal insertion present and converging to each other; anterior transverse carina absent; posterior transverse carina complete; propodeal spiracle oval. Pro- and mesotrochantellus undifferentiated; protibial spur antero-dorsally with comb and postero-dorsally with velum; protarsomeres 2–4 wider than long; pretarsal claws simple; mesotibia with two spurs, outer one slightly longer than inner; metatibia with inner margin apically without comb curved; metatibia with two spurs, outer one shorter than inner; metatarsomere 5 without hooked lobe on inner side of distal metatarsomeres of female. Forewing with areolet open, 1cu-a far distal to base of Rs&M; 2m-cu with one bulla. Hind wing with distal abscissa of Cu1 joining cu-a closer to 1A than to M.

Metasoma. Tergite I with lateral and lateromedian longitudinal carinae well developed, spiracle 0.3 of way along tergum; sternum I short, ending anterior to spiracle; laterotergite II 0.2× as wide as long; laterotergite III broad, 0.6× as wide as long; laterotergites of metasomal segments III and IV of female separated by crease; metasomal tergite VI–VIII without setae on distal margin; metasomal tergite VIII of female not folded ventrally, neither partly separated by crease, dorsally flat without hole; female with sterna IV–VI weakly sclerotized with membranous areae; female with sternum VI longer than wide, basally and distally more or less straight.

Comments. The genus contains only genotype described below. It was collected in a cloud forest in the eastern slopes of the Andes.

Etymology: The generic epithet is derived from Yanesha, an ethnic group of the Peruvian Amazon rainforest in central Peru. The gender of the genus name is neuter.

***Yanesha chorui* new species**

Fig. 20

Diagnosis. Similar to the genus, as it is a monotypic genus.

Description. ♀: Forewing length 4.7 mm.

Head. Mandibles weakly tapered, with upper tooth quite stout, lower tooth shorter and slightly less broad; malar space 0.9× as long as basal mandibular width; clypeus apical edge slightly straight, laterally slightly convex; lower face+clypeus 0.8× as long as wide, smooth (except upper 1/3 softly striate) with punctures separated by 0.5–1.0× puncture width; lateral ocellus separated from compound eye by 1.4× ocellar diameter; distance between ocelli 0.8× its own maximum diameter; head in dorsal view with gena convex them strongly rounded next to occipital carina; gena 0.8× as long as compound eyes in lateral view; frons smooth with isolate setae, softly striate around toruli; gena and vertex smooth with isolate setae; antenna with 22 flagellomeres, second flagellomere 1.4× as long as centrally broad, subapical flagellomere elongate, 1.3× as long as centrally broad, clearly longer than broad.

Mesosoma. Mesosoma generally smooth, polished and punctate; pronotum with band of setae along upper and posterior half apical margins, without wrinkle from pocket; mesoscutum with notaulus extending 0.2× length of mesoscutum, weak; mesoscutellum flat; mesopleuron without discernible mesopleural suture, except for pit anteriorly; metapleuron polished with isolated setae; submetapleural carina softly scrobiculate, anteriorly expanded into conspicuous triangular lobe. Propodeum with lateromedian longitudinal carina strong, closer distally present and fused behind posterior transverse carina; lateral longitudinal carina only present distally, enclosing area coxalis; posterior transverse carina present; propodeal spiracle about 0.6× as long as distance between these carinae. Forewing with vein 2+3rs-m 1.3× as long as abscissa of M between 3rs-m and 2m-cu. Hind wing with distal abscissa of Cu1 sclerotized throughout.

Metasoma. Metasoma with tergum I 1.4× as long as posteriorly broad, lateromedian carinae absent, smooth with punctures laterally (bare centrally); tergum II 1.0× as long as posteriorly

broad; laterotergite II about 0.2× as broad as long, rounded anteriorly; laterotergite III progressively broader, rounded apically, about 0.6× as broad as long measured apically.

Color. Head extensively yellowish except antennae, frons centrally, vertex centrally, upper – posterior (close to occipital carina) gena black. Mesosoma with mesoscutum, pronotum (except upper part yellowish) and mesopleuron (except subalar prominence yellowish and black macula below mesopleural suture) tawny, metapleuron and propodeum black, and tegula yellowish; fore legs tawny yellowish except coxa whitish cream; mid leg whitish cream except coxa basally, distal 1/3 of tibia and tarsomeres brownish; hind leg whitish cream except anterior-apical 1/3 of coxa, trochanter, basal-anterior half of femur, basal 0.1 and anterior half of tibia and tarsomeres black. Metasoma black; sterna, ovipositor and valvae brownish.

Male. Unknown

Distribution. This species was collected in a cloud forest in the eastern slopes of the Andes, in a large parch or primary forest, at 1,702m of elevation.

Etymology. The species epithet *chorui* is in honor of the Korean entomologist Choru Shin. It is a masculine noun in the genitive case.

Holotype. ♀, "PERU: PA [Pasco]. Villa Rica, Zona de Protección del Bosque San Matias San Carlos 75º12'55"W, 10º38'36"S 1702m 03-05.v.2012 Malaise trap L. Figueroa & V. Borda" (MUSM).

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APPENDICES

Appendix 1. List of the species used in the phylogenetic analysis. EM = External morphology; * = Type species of the genus.

TAXA	GEOGRAPHIC DISTRIBUTION	COLLECTION	♀	♂	EM	terminalia ♀	terminalia ♂
OUTGROUP							
Enicospilus flavoscutellatus (Brullé,1846)	Peru	MUSM, SEMC	x	x	x	x	x
Aphanistes cachil Alvarado, 2017	Peru	MUSM	x	x	x	x	x
Neliopisthus sp.	Peru	MUSM	x	x	x	x	x
Mnioes lunatus Kennedy, 1966	USA	SEMC	x	x	x	x	x
Cidaphus sp.	Nicaragua	SEMC	x	x	x	x	x
Mesochorus sp.	Peru	MUSM	x	x	x	x	x
Alexeter innoxius (Cresson, 1879)	Canada, USA	SEMC	x	x	x	x	x
Euryproctus sp.	USA	SEMC	x	x	x	x	x
Perilissus decoloratus (Cresson, 1864)	Canada, USA	SEMC	x	x	x	x	x
Phobethes sp.	USA	SEMC	x	x	x	x	x
Xenoschesis limata (Cresson, 1864)	Canada, USA	SEMC	x	x	x	x	x
INGROUP							
Aceraspis sp1	Nepal	CNC	x	x	x	x	
Aceraspis sp2	Thailand	SMNH		x	x		
Bremiella pulchella (Kriechbaumer, 1890)*		AEIC	x		x		
Bothromus bicolor Walley, 1966	Canada, USA	CNC	x		x	x	
Bothromus minoris (Davis, 1897)*	Canada	CNC, UMSP	x	x	x	x	x
Carria dreisbachi Townes & Townes, 1959	Canada, USA	SEMC	x	x	x	x	x
Chorinaeus californicus Ashmead, 1896	Canada	CNC	x	x	x	x	x
Chorinaeus cristator (Gravenhorst, 1829)	England, Sweden, Germany	CNC	x	x	x	x	x
Chorinaeus funebris (Gravenhorst, 1829)*	USA	CNC	x	x	x	x	x
Chorinaeus subcarinatus Holmgren, 1858	Canada	CNC	x	x	x	x	x
Colpotrochia cincta (Scopoli, 1763)	Germany	CNC	x	x	x	x	x
Colpotrochia watanka Gauld & Sithole, 2002	Ecuador	CNC	x	x	x	x	x
Colpotrochia sp.	Dominican Republic	CNC	x	x	x	x	x
Cubus sp1	Peru	MUSM	x	x	x	x	x
Cubus sp2	Peru	MUSM	x		x	x	
Drepanoctonus bifasciatus (Brulle, 1846)	Australia	AEIC	x	x	x		
Drepanoctonus sp.	Hungary	USNM	x				
Exochus izbus Gauld & Sithole, 2002	Costa Rica, Peru	MUSM, SEMC	x	x	x	x	x
Exochus mitratus Gravenhorst, 1829	Canada	CNC	x	x	x	x	x
Exochus spinalis Townes & Townes, 1959	Costa Rica, Mexico	CNC	x	x	x	x	x
Exochus tegularis Ashmead, 1894	Martinique, Saint Lucia	CNC	x	x	x	x	x
Exochus sp	USA	SEMC	x	x	x	x	x
Exochus sp 6	Peru	MUSM	x	x	x	x	x
Exochus CNC1	Mexico	CNC	x	x	x	x	x
Finisterra rubrum sp. nov.	Chile	CNC	x	x	x	x	x
Finisterra B5	Chile	CNC	x	x	x	x	x
Finisterra B9	Chile	AEIC	x	x	x	x	x
Forrestopius judyae Gauld & Sithole, 2002*	Costa Rica	MNCR	x		x		
Forrestopius larryi Gauld & Sithole, 2002	Costa Rica	BMNH	x	x	x		

Forrestopius pamelae Gauld & Sithole, 2002	Costa Rica	BMNH, MNCR	x	x	x		
Forrestopius AEIC4	Ecuador	AEIC	x		x		
Forrestopius CNC7	Ecuador	CNC	x		x		
Forrestopius sp4	Peru	MUSM	x		x	x	
Hemimetopius angulitarsis Benoit, 1955	Cameroon, Malawi, Uganda, Zimbabwe	AEIC, BMNH	x	x	x	x	x
Hemimetopius sp.	Zimbabwe	BMNH	x		x		
Huetzin acarinatus sp. nov.	Mexico	AEIC	x	x	x		
Hypsicera curvator (Fabricius, 1793)	Canada	CNC	x		x		
Hypsicera femoralis (Geoffrou, 1785)*	USA	UMSP	x	x	x	x	x
Hypsicera CNC1	Japan	CNC	x	x	x		x
Hypsicera sp.	Peru	MUSM	x		x	x	x
Stethoncus arcticus Townes & Townes, 1959*	Canada	CNC	x	x	x	x	x
Stethoncus AEIC1	Ecuador	AEIC	x	x	x		
Ischyrocnemis goesi Holmgren, 1858*	Sweden	AEIC	x		x		x
Jirajara yacambuensis sp. nov.	Venezuela	AEIC	x	x	x		
Lapton femoralis Nees, 1816*	Hungary	AEIC		x	x		x
Leurus angustignathus Herrera, 2013	Brazil	CNC	x	x	x	x	x
Leurus caeruliventris (Cresson, 1868)*	Costa Rica, Ecuador, Peru	CNC, MUSM	x	x	x	x	x
Leurus fascialis Gauld & Sithole, 2002	Costa Rica	CNC	x		x	x	
Leurus xalifer Gauld & Sithole, 2002	Costa Rica	MNCR	x		x		
Leurus MUSM2	Peru	MUSM	x		x	x	
Leurus sp6	Dominican Republic	CNC	x	x	x	x	x
Leurus A9	Peru	MUSM	x	x	x	x	x
Leurus A10	Peru	MUSM	x	x	x		x
Leurus AEIC3	Ecuador	AEIC	x		x		
Leurus AEIC4	Ecuador	AEIC	x		x		
Macromalon montanum Townes & Townes, 1959	Canada	CNC	x	x	x	x	x
Metopius dentatus (Fabricius, 1779)	Austria	CNC	x	x	x	x	x
Metopius pollinctorius (Say, 1835)	Canada	CNC	x	x	x	x	x
Ojuelus juachicus Khalaim & Ruíz-Cancino, 2012*	Mexico	UAT	x		x		
Periope aethiops (Cresson, 1868)	USA	UMSP		x		x	x
Periope auscultator Haliday, 1838 *	Palearctic	USNM	x	x	x		
Pseudometopius hagenii (Cresson, 1872)*	USA	SEMC	x	x	x	x	x
Sciron sp1	Tasmania	BMNH	x	x	x	x	x
Sciron sp2	Tasmania	BMNH	x	x	x	x	x
Scolomus borealis (Townes, 1971)	England	BMNH	x		x		
Scolomus megallanicus Walkley, 1962	Chile	AEIC, USNM	x	x	x		
Scolomus viridis Townes & Townes, 1950*	Argentina	USNM		x	x		
Scolomus sp.	Peru	MUSM	x		x		
Seticornuta albopilosa (Cameron, 1907)*	China, Myanmar	USNM	x	x	x		
Seticornuta cortesi Porter, 1998	Chile	AEIC	x		x		
Seticornuta terminalis (Ashmead, 1896)	USA	SEMC, UMSP	x	x	x	x	x
Seticornuta Brazil	Brazil	CNC	x	x	x	x	x
Seticornuta Guadalcanal	Guadalcanal	SEMC		x	x		x
Spudaeus indigus (Davis, 1897)	Canada	CNC, SEMC	x	x	x	x	x
Spudaeus scaber (Gravenhorst, 1829)	Canada	CNC	x	x	x	x	x
Synosis clepsidra Townes & Townes, 1950*	USA	SEMC, UMSP	x	x	x	x	x

Synosis sp.	Brazil	CNC	x	x	x	x	
Triclistus cholo Alvarado & Rodriguez-Berrio, 2013	Peru	MUSM	x	x	x	x	x
Triclistus emarginalus (Say, 1829)	USA	UMSP	x	x	x	x	x
Triclistus occidentis Townes & Townes, 1959	USA	UMSP	x	x	x	x	x
Trieces bicalcaratus (Benoit, 1855)	Uganda	AEIC, SEMC	x	x	x		x
Trieces flavifrons (Ashmead, 1890)	USA	UMSP	x	x	x	x	x
Trieces horisme Gauld & Sithole, 2002	Mexico, Peru	CNC, MUSM	x	x	x	x	x
Trieces peruanus Tolkanitz, 2009	Peru	MUSM	x	x	x	x	x
Trieces tyloides Mazon & Bordera, 2016	Brazil	CNC	x	x	x	x	x
Wira luisi sp. nov.	Peru	MUSM, SEMC		x	x		x
Wira AEICE	Ecuador	AEIC		x	x		
Wira AEICF	Ecuador	AEIC		x	x		
Wiracocha C1	Ecuador	AEIC		x	x		x
Yanesha chorui sp. nov.	Peru	MUSM	x		x	x	

Appendix 2. Character matrix used in the phylogenetic analyses of Metopiinae. Dash (–) = not applicable; question marks (?) were used when the characters could not be codified.

	Characters														
Taxa	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Enicospilus flavoscutellatus	0	0	–	–	0	0	0	0	0	0	0	0	0	–	0
Aphanistes cachil	0	0	–	–	0	0	1	0	1	0	0	0	0	–	0
Mnioes lunatus	0	0	–	–	0	0	2	0	0	0	0	0	0	–	0
Cidaphus sp	0	0	–	–	0	0	2	0	0	0	0	0	0	–	0
Mesochorus sp	0	0	–	–	0	0	2	0	1	0	0	0	0	–	0
Alexeter innoxius	1	0	–	–	0	0	2	0	0	0	0	0	0	–	0
Euryproctus sp	1	0	–	–	0	0	2	0	0	0	0	0	0	–	0
Perilissus decoloratus	1	0	–	–	0	0	0	0	0	0	0	0	0	–	0
Phobetes sp	1	0	–	–	0	0	2	0	0	0	0	0	0	–	0
Xenoschesis limata	1	0	–	–	0	0	2	0	0	0	0	0	0	–	0
Neliopisthus sp	0	0	–	–	0	0	2	0	0	0	0	0	0	–	0
Aceraspis sp1	1	1	1	1	2	0	2	0	0	0	1	0	0	–	0
Aceraspis sp2	1	1	?	1	2	0	2	0	0	0	1	0	0	–	0
Bremiella pulchella	0	1	0	?	?	0	2	0	0	0	0	0	0	–	0
Bothromus bicolor	0	1	0	?	?	0	0	0	0	0	0	0	1	0	0
Bothromus minoris	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Carria dreisbachi	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0
Chorinaeus californicus	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Chorinaeus cristator	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Chorinaeus funebris	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Chorinaeus subcarinatus	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Colpotrochia cincta	0	1	0	0	1	0	2	0	0	1	0	0	0	–	1
Colpotrochia watanka	0	1	0	0	1	0	0	0	0	1	0	0	0	–	1
Colpotrochia sp	0	1	0	0	1	0	0	0	0	1	0	0	0	–	1
Cubus sp1	0	1	0	0	1	1	–	–	2	1	0	0	0	–	1
Cubus sp2	0	1	0	?	?	1	–	–	2	1	0	0	0	–	1
Drepanoctonus bifasciatus	0	1	0	0	1	0	2	0	1	0	?	0	0	–	0
Drepanoctomus sp	0	1	0	?	?	0	1	0	1	0	0	0	0	–	0
Exochus izbus	0	1	0	0	1	0	1	0	1	0	0	0	0	–	0
Exochus mitratos	0	1	1	1	2	0	2	0	1	0	0	0	0	–	0
Exochus spinalis	0	1	0	0	1	0	2	0	1	0	0	0	0	–	0
Exochus tegularis	0	1	0	0	1	0	1	0	1	0	0	0	0	–	0
Exochus sp	0	1	0	0	1	0	2	0	1	0	0	0	0	–	0
Exochus sp6	0	1	0	0	1	0	1	0	1	0	0	0	0	–	0
Exochus CNC1	0	1	0	0	1	0	2	0	1	0	0	0	0	–	0
Finisterra rubra	0	1	0	0	1	0	0	0	0	0	0	0	0	–	1
Finisterra B5	0	1	0	0	1	0	0	0	0	0	0	0	0	–	1
Finisterra B9	0	1	0	0	1	0	0	0	0	0	0	0	0	–	1
Forrestopius judyae	0	1	2	?	?	2	2	0	0	1	0	0	1	0	0
Forrestopius larryi	0	1	0	0	1	0	2	0	0	1	0	1	1	0	0
Forrestopius pamelae	0	1	2	0	1	0	2	0	0	1	0	0	1	0	0
Forrestopius AEIC4	0	1	2	?	?	0	2	0	0	1	0	0	1	0	0
Forrrestopius CNC7	0	1	2	?	?	0	2	0	0	1	0	0	1	0	0
Forrrestopius sp4	0	1	0	?	?	0	2	0	0	1	0	0	1	0	0
Hemimetopius angulitarsus	0	1	0	0	1	0	1	0	0	0	0	0	0	–	0
Hemimetopius sp	0	1	0	?	?	0	1	0	0	0	0	0	0	–	0
Huetzin acarinatus	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0
Hypsicera curvator	0	1	2	2	3	0	2	0	1	0	0	0	0	–	0

Hypsicera femoralis	0	1	2	0	1	0	2	0	1	0	0	0	0	–	0
Hypsicera CNC1	0	1	0	0	1	1	–	–	2	0	0	0	0	–	0
Hypsicera 2	0	1	0	?	?	0	2	0	1	0	0	0	0	–	0
Hypsicera (Stethoncus) articus	0	1	2	0	1	0	2	1	0	0	0	0	0	–	0
Hypsicera (*Stethoncus)* AEIC1	0	1	2	?	?	0	2	1	0	0	0	0	0	–	0
Ischyrocnemis goesi	0	1	0	?	?	0	2	0	0	0	0	0	?	?	0
Jirajara yacambuensis	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0
Lapton femoralis	0	1	?	0	1	1	–	–	0	0	0	0	0	–	?
Leurus angustignathus	0	1	2	0	1	0	2	0	3	1	0	0	1	1	0
Leurus cauriventris	0	1	1	0	1	0	2	0	3	1	0	0	1	1	0
Leurus fascialis	0	1	0	?	?	0	2	0	0	1	0	1	1	0	0
Leurus xalifer	0	1	0	?	?	0	2	0	0	1	0	1	1	0	0
Leurus MUSM2	0	1	0	?	?	0	2	0	3	1	0	0	1	1	0
Leurus sp6	0	1	1	0	1	0	2	0	3	1	0	0	1	1	0
Leurus A9	0	1	0	0	1	0	2	0	0	1	0	1	1	0	0
Leurus A10	0	1	0	0	1	0	2	0	0	1	0	1	1	0	0
Leurus AEIC3	0	1	0	?	?	0	2	0	0	1	0	1	1	0	0
Leurus AEIC4	0	1	0	?	?	0	2	0	0	1	0	0	1	1	0
Macromalon montanum	0	1	0	0	1	0	2	0	2	1	0	0	1	0	0
Metopius dentatus	1	1	1	1	2	0	1	0	1	0	0	0	0	–	0
Metopius pollictorius	1	1	1	1	2	0	1	0	1	0	0	0	0	–	0
Ojuelus juachicus	0	1	0	?	?	0	2	0	0	0	0	0	0	–	1
Periope auscultator	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Periope aethiops	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Pseudometopius hagenii	1	1	1	1	2	0	2	0	1	0	0	0	0	–	0
Sciron A17	0	1	0	0	1	0	2	0	0	1	0	0	0	–	0
Sciron sp	0	1	0	0	1	0	2	0	0	1	0	0	0	–	0
Scolomus borealis	0	0	–	–	?	0	2	0	1	0	0	0	0	–	0
Scolomus magellanicus	0	0	–	–	0	0	2	0	1	0	0	0	0	–	0
Scolomus viridis	0	0	–	–	0	0	2	0	1	0	0	0	0	–	0
Scolomus sp	0	0	–	–	?	0	2	0	1	0	0	0	0	–	0
Seticornuta albopilosa	0	1	2	2	3	0	2	0	0	1	0	0	0	–	0
Seticornuta cortesi	0	1	0	?	?	0	2	0	0	1	0	0	0	–	0
Seticornuta terminalis	0	1	0	0	1	0	2	0	0	1	0	0	0	–	0
Seticornuta Brazil	0	1	0	0	1	0	2	0	0	1	0	0	0	–	0
Seticornuta Guadalcanal	0	1	?	2	3	0	2	0	0	1	0	0	0	–	0
Spudaeus indigus	1	1	0	0	1	0	2	0	1	0	0	0	0	–	0
Spudaeus scaber	1	1	0	0	1	0	2	0	1	0	0	0	0	–	0
Synosis clepsidra	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Synosis sp	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Triclistus cholo	0	1	0	0	1	0	2	0	1	0	0	0	0	–	0
Triclistus emarginalus	0	1	0	0	1	0	2	0	1	0	0	0	0	–	0
Triclistus occidentis	0	1	0	0	1	0	2	0	1	0	0	0	0	–	0
Trieces bicalcaratus	0	3	2	0	1	0	2	0	0	0	0	0	0	–	0
Trieces flavifrons	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Trieces horisme	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Trieces peruvianus	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Trieces tyloides	0	1	0	0	1	0	2	0	0	0	0	0	0	–	0
Wira luisi	0	1	?	0	1	0	2	0	0	1	0	0	1	0	0
Wira AEICE	0	1	?	0	1	0	2	0	0	1	0	0	1	0	0
Wira AEICF	0	1	?	0	1	0	2	0	0	1	0	0	1	0	0
Wira C5	0	1	?	0	1	0	2	0	0	1	0	0	1	0	0
Yanesha chorui	0	1	0	?	?	0	2	0	0	1	0	0	0	–	0

Continuing Appendix 2

Taxa	Characters 15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Enicospilus flavoscutellatus	0	–	0	0	0	0	0	0	0	0	0	–	0	0	0
Aphanistes cachil	0	–	0	0	0	0	0	1	1	0	0	–	0	0	0
Mnioes lunatus	0	–	0	0	0	0	0	0	1	0	0	–	0	0	0
Cidaphus sp	0	–	0	0	0	0	0	0	1	0	0	–	0	0	1
Mesochorus sp	0	–	0	0	0	0	0	0	1	0	0	–	0	0	2
Alexeter innoxius	0	–	0	0	0	0	0	0	0	0	1	–	0	0	0
Euryproctus sp	0	–	0	0	0	0	0	0	1	0	1	–	0	0	0
Perilissus decoloratus	0	–	0	0	0	0	0	0	1	0	1	–	0	0	0
Phobetes sp	0	–	0	0	0	0	0	0	1	0	1	–	0	0	1
Xenoschesis limata	0	–	0	0	0	0	0	0	1	0	1	–	0	0	1
Neliopisthus sp	0	–	0	0	0	0	0	0	1	0	1	–	0	0	1
Aceraspis sp1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0
Aceraspis sp2	1	0	?	0	?	0	?	0	1	1	0	0	1	0	0
Bremiella pulchella	0	–	0	?	0	?	0	0	1	1	0	0	0	0	0
Bothromus bicolor	0	–	0	0	0	0	0	0	1	1	0	0	0	0	0
Bothromus minoris	0	–	0	0	0	0	0	0	1	1	0	0	0	0	0
Carria dreisbachi	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Chorinaeus californicus	?	?	0	0	0	0	0	0	1	1	0	0	0	0	0
Chorinaeus cristator	?	?	0	0	0	0	0	0	1	1	0	0	0	0	0
Chorinaeus funebris	?	?	0	0	0	0	0	0	1	1	0	0	0	0	0
Chorinaeus subcarinatus	?	?	0	0	1	0	1	0	1	1	0	0	0	0	0
Colpotrochia cincta	0	–	0	0	0	0	0	0	0	1	0	1	0	0	0
Colpotrochia watanka	0	–	0	0	0	0	0	0	0	1	0	1	0	0	0
Colpotrochia sp	0	–	0	0	0	0	0	0	0	1	0	1	0	0	0
Cubus sp1	0	–	0	0	0	0	0	0	0	1	0	1	0	0	0
Cubus sp2	0	–	0	?	0	?	0	0	0	1	0	1	0	0	0
Drepanoctonus bifasciatus	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Drepanoctomus sp	1	0	0	?	0	?	0	0	1	1	0	0	0	0	0
Exochus izbus	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Exochus mitratos	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Exochus spinalis	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Exochus tegularis	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Exochus sp	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Exochus sp6	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Exochus CNC1	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Finisterra rubra	0	–	0	0	0	0	0	0	0	1	0	1	0	0	0
Finisterra B5	0	–	0	0	0	0	0	0	0	1	0	1	0	0	0
Finisterra B9	0	–	0	0	0	0	0	0	0	1	0	1	0	0	0
Forrestopius judyae	0	–	0	?	0	?	0	0	1	1	0	0	0	0	2
Forrestopius larryi	0	–	1	1	0	0	0	1	1	1	0	0	0	0	2
Forrestopius pamelae	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Forrestopius AEIC4	0	–	0	?	0	?	0	0	1	1	0	0	0	0	2
Forrrestopius CNC7	0	–	0	?	0	?	0	0	1	1	0	0	0	0	2
Forrrestopius sp4	0	–	0	?	0	?	0	0	1	1	0	0	0	0	2
Hemimetopius angulitarsus	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Hemimetopius sp	1	1	0	?	0	?	0	0	1	1	0	0	0	0	0
Huetzin acarinatus	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Hypsicera curvator	0	–	0	0	0	0	0	0	1	1	0	0	0	0	1
Hypsicera femoralis	0	–	0	0	0	0	0	0	1	1	0	0	0	0	1
Hypsicera CNC1	0	–	0	0	0	0	0	0	1	1	0	0	0	0	0
Hypsicera 2	0	–	0	0	0	0	0	0	1	1	0	0	0	0	1
Hypsicera Stethoncus articus	0	–	0	0	0	0	0	0	1	1	0	0	0	0	1

Hypsicera Stethoncus AEIC1	0	–	0	?	0	0	0	0	1	1	0	0	0	0	1
Ischyrocnemis goesi	0	–	0	?	0	?	0	0	1	1	0	0	0	0	0
Jirajara yacambuensis	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Lapton femoralis	0	?	0	0	0	0	0	0	0	1	0	?	0	0	0
Leurus angustignathus	0	–	0	0	0	0	0	1	1	1	0	0	0	0	2
Leurus cauriventris	0	–	0	0	0	0	0	1	1	1	0	0	0	0	2
Leurus fascialis	0	–	0	?	0	?	0	1	1	1	0	0	0	0	2
Leurus xalifer	0	–	1	?	0	?	0	1	1	1	0	0	0	0	2
Leurus MUSM2	0	–	0	?	0	?	0	1	1	1	0	0	0	0	2
Leurus sp6	0	–	0	0	0	0	0	1	1	1	0	0	0	0	2
Leurus A9	0	–	1	1	0	0	0	1	1	1	0	0	0	0	2
Leurus A10	0	–	1	1	0	0	0	1	1	1	0	0	0	0	2
Leurus AEIC3	0	–	0	?	0	?	0	0	1	1	0	0	0	0	2
Leurus AEIC4	0	–	0	?	0	?	0	1	1	1	0	0	0	0	2
Macromalon montanum	0	–	0	0	0	0	0	0	1	1	0	0	0	0	1
Metopius dentatus	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0
Metopius pollictorius	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0
Ojuelus juachicus	0	–	0	?	0	?	0	0	0	1	0	1	0	0	0
Periope auscultator	0	–	0	0	0	0	0	0	0	1	0	0	0	0	1
Periope aethiops	0	–	0	0	0	0	0	0	0	1	0	0	0	0	1
Pseudometopius hagenii	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Sciron A17	0	–	0	0	0	0	0	0	1	1	0	0	0	0	1
Sciron sp	0	–	0	0	0	0	0	0	1	1	0	0	0	0	1
Scolomus borealis	0	–	0	?	0	?	0	?	1	1	0	0	0	0	0
Scolomus magellanicus	0	–	0	0	0	0	0	0	1	0	0	0	0	0	0
Scolomus viridis	0	–	?	0	?	0	?	0	1	0	0	0	0	0	0
Scolomus sp	0	–	0	?	0	?	0	0	1	1	0	0	0	0	0
Seticornuta albopilosa	0	–	0	0	0	0	0	0	1	1	0	0	0	0	0
Seticornuta cortesi	0	–	0	?	0	?	0	0	1	1	0	0	0	0	0
Seticornuta terminalis	0	–	0	0	0	0	0	0	0	1	0	0	0	0	0
Seticornuta Brazil	0	–	0	0	0	0	0	0	0	1	0	0	0	0	0
Seticornuta Guadalcanal	0	–	?	0	?	0	?	0	1	1	0	0	0	0	0
Spudaeus indigus	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Spudaeus scaber	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Synosis clepsidra	0	–	0	0	0	0	0	0	1	1	0	0	0	0	0
Synosis sp	0	–	0	0	0	0	0	0	1	1	0	0	0	0	0
Triclistus cholo	0	–	0	0	0	0	0	1	1	1	0	1	0	0	1
Triclistus emarginalus	0	–	0	0	0	0	0	0	1	1	0	1	0	0	1
Triclistus occidentis	0	–	0	0	0	0	0	0	1	1	0	1	0	0	1
Trieces bicalcaratus	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Trieces flavifrons	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Trieces horisme	1	1	0	0	1	0	1	0	1	1	0	0	0	0	0
Trieces peruvianus	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0
Trieces tyloides	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Wira luisi	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Wira AEICE	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Wira AEICF	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Wira C5	0	–	0	0	0	0	0	0	1	1	0	0	0	0	2
Yanesha chorui	0	–	0	?	0	?	0	0	1	1	0	0	0	0	0

Continuing Appendix 2

Taxa	Characters														
	30	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**
Enicospilus flavoscutellatus	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Aphanistes cachil	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Mnioes lunatus	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Cidaphus sp	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Mesochorus sp	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Alexeter innoxius	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Euryproctus sp	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Perilissus decoloratus	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Phobetes sp	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Xenoschesis limata	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Neliopisthus sp	0	0	0	0	–	–	–	0	–	0	0	–	0	0	0
Aceraspis sp1	0	0	0	1	1	–	–	0	–	0	2	0	0	0	0
Aceraspis sp2	0	0	0	1	1	–	–	0	–	0	2	0	0	0	0
Bremiella pulchella	0	0	0	1	0	2	–	0	–	0	0	–	0	0	0
Bothromus bicolor	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Bothromus minoris	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Carria dreisbachi	0	0	0	1	0	0	0	1	0	1	3	–	0	0	0
Chorinaeus californicus	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Chorinaeus cristator	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Chorinaeus funebris	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Chorinaeus subcarinatus	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Colpotrochia cincta	0	0	0	1	1	–	–	0	–	0	2	0	0	0	0
Colpotrochia watanka	0	0	0	1	1	–	–	0	–	0	0	–	0	0	0
Colpotrochia sp	0	0	0	1	1	–	–	0	–	0	0	–	0	0	0
Cubus sp1	0	0	0	1	1	–	–	0	–	0	0	–	0	1	0
Cubus sp2	0	0	0	1	1	–	–	0	–	0	0	–	0	1	0
Drepanoctonus bifasciatus	0	0	0	1	1	–	–	0	–	0	0	–	0	0	0
Drepanoctomus sp	0	0	0	1	1	–	–	0	–	0	0	–	0	0	0
Exochus izbus	0	0	0	1	0	1	0	0	–	0	3	–	0	0	0
Exochus mitratos	0	0	0	1	0	1	0	0	–	0	2	0	0	0	0
Exochus spinalis	0	0	0	1	0	1	0	0	–	0	4	0	0	0	0
Exochus tegularis	0	0	0	1	0	1	0	0	–	0	3	–	0	0	0
Exochus sp	0	0	0	1	0	1	0	0	–	0	4	0	0	0	0
Exochus sp6	0	0	0	1	0	1	0	0	–	0	3	–	0	0	0
Exochus CNC1	0	0	1	1	0	1	0	0	–	0	4	0	0	0	0
Finisterra rubra	0	0	0	1	1	–	–	0	–	0	2	1	0	0	0
Finisterra B5	0	0	0	1	1	–	–	0	–	0	2	1	0	0	0
Finisterra B9	0	0	0	1	1	–	–	0	–	0	2	1	0	0	0
Forrestopius judyae	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Forrestopius larryi	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Forrestopius pamelae	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Forrestopius AEIC4	1	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Forrrestopius CNC7	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Forrrestopius sp4	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Hemimetopius angulitarsus	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Hemimetopius sp	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Huetzin acarinatus	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Hypsicera curvator	0	0	1	1	0	0	0	0	–	0	3	–	0	0	0
Hypsicera femoralis	0	0	0	1	0	0	0	0	–	0	3	–	0	0	0
Hypsicera CNC1	0	0	0	1	0	0	0	0	–	0	3	–	0	0	0
Hypsicera 2	0	0	1	1	0	0	0	0	–	0	3	0	0	0	0
Hypsicera (Stethoncus) articus	0	1	1	1	0	0	0	0	–	0	4	0	0	0	0
Hypsicera (Stethoncus)	0	1	1	1	0	0	0	0	–	0	4	0	0	0	0

AEIC1															
Ischyrocnemis goesi	0	0	0	0	–	–	–	0	–	0	0	–	0	0	?
Jirajara yacambuensis	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Lapton femoralis	0	0	0	1	1	–	–	?	?	?	0	–	0	0	?
Leurus angustignathus	0	0	0	1	0	0	0	1	1	0	2	0	1	0	0
Leurus cauriventris	0	0	0	1	0	0	0	1	1	0	2	0	1	0	0
Leurus fascialis	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Leurus xalifer	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Leurus MUSM2	0	0	0	1	0	0	0	1	0	1	2	0	1	0	0
Leurus sp6	0	0	0	1	0	0	0	1	1	0	2	0	1	0	0
Leurus A9	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Leurus A10	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Leurus AEIC3	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Leurus AEIC4	0	0	0	1	0	0	0	1	0	1	2	0	1	0	0
Macromalon montanum	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0
Metopius dentatus	0	0	0	1	1	–	–	0	–	0	0	–	0	0	1
Metopius pollictorius	0	0	0	1	1	–	–	0	–	0	0	–	0	0	1
Ojuelus juachicus	0	0	0	1	1	–	–	0	–	0	2	0	?	0	0
Periope auscultator	0	0	0	1	1	–	–	2	–	0	2	0	0	0	0
Periope aethiops	0	0	0	1	1	–	–	2	–	0	2	0	0	0	0
Pseudometopius hagenii	0	0	0	1	1	–	–	0	–	0	2	0	0	0	0
Sciron A17	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Sciron sp	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Scolomus borealis	0	0	0	0	–	–	–	0	–	0	2	0	0	0	0
Scolomus magellanicus	0	0	0	0	–	–	–	0	–	0	2	0	0	0	0
Scolomus viridis	0	0	0	0	–	–	–	0	–	0	2	0	0	0	0
Scolomus sp	0	0	0	0	–	–	–	0	–	0	2	0	0	0	0
Seticornuta albopilosa	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0
Seticornuta cortesi	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0
Seticornuta terminalis	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0
Seticornuta Brazil	0	0	0	1	0	0	0	1	1	0	0	–	0	0	0
Seticornuta Guadalcanal	0	0	0	1	0	0	0	1	1	0	2	0	0	0	0
Spudaeus indigus	0	0	0	1	0	2	0	0	–	0	2	0	0	0	0
Spudaeus scaber	0	0	0	1	0	2	0	0	–	0	2	0	0	0	0
Synosis clepsidra	0	0	0	1	0	0	1	0	–	0	3	–	0	0	0
Synosis sp	0	0	0	1	0	0	1	0	–	0	3	–	0	0	0
Triclistus cholo	0	0	0	1	1	–	–	0	–	0	0	–	0	0	0
Triclistus emarginalus	0	0	0	1	1	–	–	0	–	0	0	–	0	0	0
Triclistus occidentis	0	0	0	1	1	–	–	0	–	0	0	–	0	0	0
Trieces bicalcaratus	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Trieces flavifrons	0	0	0	1	0	0	0	0	–	0	2	0	0	0	0
Trieces horisme	0	0	0	1	0	0	0	0	–	0	2	0	0	0	1
Trieces peruvianus	0	0	0	1	0	0	0	0	–	0	2	0	0	0	1
Trieces tyloides	0	0	0	1	0	0	0	0	–	0	2	0	0	0	1
Wira luisi	1	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Wira AEICE	1	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Wira AEICF	1	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Wira C5	1	0	0	1	0	0	0	1	0	1	2	0	0	0	0
Yanesha chorui	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0

Continuing Appendix 2

Taxa	Characters														
	45	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**
Enicospilus flavoscutellatus	0	0	–	0	0	0	0	–	0	0	?	0	0	0	0
Aphanistes cachil	0	0	–	0	0	0	0	–	0	1	?	0	0	0	1
Mnioes lunatus	0	0	–	0	0	0	0	–	0	0	?	0	0	0	0
Cidaphus sp	0	1	0	0	0	0	1	0	0	0	?	0	0	0	0
Mesochorus sp	0	1	0	0	0	0	1	1	0	0	?	0	0	0	1
Alexeter innoxius	0	0	–	0	0	0	0	–	0	0	?	0	0	0	0
Euryproctus sp	0	0	–	0	0	0	0	–	0	0	?	0	0	0	0
Perilissus decoloratus	0	1	0	0	0	0	0	–	0	0	?	0	0	0	0
Phobetes sp	0	0	–	0	0	0	0	–	0	0	?	0	0	0	0
Xenoschesis limata	0	1	0	0	0	0	0	0	1	0	?	0	0	0	0
Neliopisthus sp	0	1	0	0	0	0	0	–	0	0	?	0	0	0	0
Aceraspis sp1	0	0	–	0	1	1	1	0	1	0	?	0	1	0	1
Aceraspis sp2	0	0	–	0	1	1	1	0	1	0	?	0	1	0	1
Bremiella pulchella	0	0	–	0	0	1	1	0	2	0	?	0	1	0	1
Bothromus bicolor	0	1	0	0	1	1	1	0	1	0	?	0	1	0	1
Bothromus minoris	0	1	0	0	1	1	1	0	1	0	?	0	1	0	1
Carria dreisbachi	0	0	–	0	0	1	1	1	0	0	?	0	1	0	1
Chorinaeus californicus	0	0	–	0	1	1	1	0	1	1	?	0	1	0	1
Chorinaeus cristator	0	0	–	0	1	1	1	0	1	1	?	0	1	0	1
Chorinaeus funebris	0	0	–	0	1	1	1	0	0	1	?	0	1	0	1
Chorinaeus subcarinatus	0	0	–	0	1	1	1	0	0	1	?	0	1	0	1
Colpotrochia cincta	0	1	1	0	0	1	1	0	0	0	?	0	1	0	1
Colpotrochia watanka	0	1	1	0	0	1	1	0	0	0	?	0	1	0	1
Colpotrochia sp	0	1	1	0	0	1	1	0	0	0	?	0	1	0	1
Cubus sp1	1	1	2	1	0	1	1	0	0	0	?	0	1	0	1
Cubus sp2	1	1	2	1	0	1	1	0	0	0	?	0	1	0	1
Drepanoctonus bifasciatus	0	0	–	0	1	1	1	0	1	0	0	0	1	0	1
Drepanoctomus sp	0	0	–	0	1	1	1	0	1	0	0	0	1	0	1
Exochus izbus	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Exochus mitratos	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Exochus spinalis	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Exochus tegularis	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Exochus sp	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Exochus sp6	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Exochus CNC1	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Finisterra rubra	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Finisterra B5	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Finisterra B9	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Forrestopius judyae	0	1	0	0	0	1	1	1	0	0	?	0	1	0	1
Forrestopius larryi	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Forrestopius pamelae	0	1	0	0	0	1	1	1	0	0	?	0	1	0	1
Forrestopius AEIC4	0	1	0	0	0	1	1	1	0	0	?	0	1	0	1
Forrrestopius CNC7	0	1	0	0	0	1	1	1	0	0	?	0	1	0	1
Forrrestopius sp4	0	0	–	0	0	1	1	1	0	0	?	0	1	0	1
Hemimetopius angulitarsus	0	0	–	0	1	1	1	0	1	0	?	0	1	0	1
Hemimetopius sp	0	0	–	0	1	1	1	0	1	0	?	0	1	0	1
Huetzin acarinatus	0	0	–	0	0	1	1	1	0	0	?	0	1	0	1
Hypsicera curvator	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Hypsicera femoralis	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Hypsicera CNC1	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Hypsicera 2	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Hypsicera (Stethoncus)	2	1	0	0	1	1	1	0	0	0	?	1	1	0	1

articus															
Hypsicera (Stethoncus) AEIC1	2	1	0	0	1	1	1	0	0	0	?	1	1	0	1
Ischyrocnemis goesi	0	1	0	0	1	0	1	0	0	0	?	0	1	0	1
Jirajara yacambuensis	0	0	–	0	0	1	1	1	0	0	?	0	1	0	1
Lapton femoralis	0	1	0	0	?	0	0	–	2	0	?	0	1	0	1
Leurus angustignathus	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Leurus cauriventris	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Leurus fascialis	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Leurus xalifer	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Leurus MUSM2	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Leurus sp6	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Leurus A9	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Leurus A10	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Leurus AEIC3	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Leurus AEIC4	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Macromalon montanum	0	1	0	0	?	1	1	0	1	0	?	0	1	0	1
Metopius dentatus	0	1	0	0	1	0	1	0	1	0	?	0	1	0	1
Metopius pollictorius	0	1	0	0	1	0	1	0	1	0	?	0	1	0	1
Ojuelus juachicus	0	1	1	0	0	1	1	0	0	0	?	0	1	0	1
Periope auscultator	0	0	–	0	1	1	1	0	1	0	1	0	1	0	1
Periope aethiops	0	0	–	0	1	1	1	0	1	0	1	0	1	0	1
Pseudometopius hagenii	0	0	–	0	1	0	1	0	1	0	?	0	1	0	1
Sciron A17	0	0	–	0	0	1	1	1	0	0	?	0	1	0	1
Sciron sp	0	0	–	0	0	1	1	1	0	0	?	0	1	0	1
Scolomus borealis	0	0	–	0	0	0	1	1	0	0	?	0	0	0	1
Scolomus magellanicus	0	1	0	0	0	0	0	–	0	0	?	0	0	0	0
Scolomus viridis	0	1	0	0	0	0	0	–	0	0	?	0	0	0	0
Scolomus sp	0	0	–	0	0	0	1	1	0	0	?	0	0	0	1
Seticornuta albopilosa	0	0	–	0	0	1	1	0	2	0	0	0	1	0	1
Seticornuta cortesi	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Seticornuta terminalis	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Seticornuta Brazil	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1
Seticornuta Guadalcanal	0	0	–	0	0	1	1	0	2	0	0	0	1	0	1
Spudaeus indigus	0	1	0	0	1	0	1	0	1	0	?	0	1	1	0
Spudaeus scaber	0	1	0	0	1	0	1	0	1	0	?	0	1	1	0
Synosis clepsidra	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Synosis sp	0	1	0	0	1	1	1	0	0	0	?	0	1	0	1
Triclistus cholo	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Triclistus emarginalus	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Triclistus occidentis	0	1	0	0	0	1	1	0	0	0	?	0	1	0	1
Trieces bicalcaratus	0	0	–	0	1	1	0	–	0	0	?	0	1	0	1
Trieces flavifrons	0	0	–	0	1	1	0	–	0	0	?	0	1	0	1
Trieces horisme	0	0	–	0	1	1	0	–	0	1	?	0	1	0	1
Trieces peruvianus	0	0	–	0	1	1	0	–	0	1	?	0	1	0	1
Trieces tyloides	0	0	–	0	1	1	0	–	0	1	?	0	1	0	1
Wira luisi	0	1	0	0	0	1	1	1	0	2	?	0	1	0	1
Wira AEICE	0	1	0	0	0	1	1	1	0	2	?	0	1	0	1
Wira AEICF	0	1	0	0	0	1	1	1	0	2	?	0	1	0	1
Wira C5	0	1	0	0	0	1	1	1	0	2	?	0	1	0	1
Yanesha chorui	0	0	–	0	0	1	1	0	0	0	?	0	1	0	1

Continuing Appendix 2

Taxa	Characters														
	60	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**
Enicospilus flavoscutellatus	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0
Aphanistes cachil	0	0	0	1	–	–	0	0	1	0	0	2	0	0	0
Mnioes lunatus	0	0	0	1	–	–	1	0	0	0	0	2	0	0	0
Cidaphus sp	0	0	0	1	–	–	0	0	0	0	0	1	0	0	0
Mesochorus sp	0	0	0	1	–	–	0	0	0	0	0	1	0	0	0
Alexeter innoxius	0	0	0	1	–	–	0	0	0	0	0	2	0	0	0
Eurycproctus sp	0	0	0	1	–	–	1	0	1	0	0	2	0	0	0
Perilissus decoloratus	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Phobetes sp	0	0	0	1	–	–	0	0	0	0	0	2	0	0	0
Xenoschesis limata	0	0	0	1	–	–	0	0	0	0	0	2	0	0	0
Neliopisthus sp	0	0	0	1	–	–	1	0	0	0	0	1	0	0	0
Aceraspis sp1	1	0	1	0	1	1	1	0	0	0	1	0	0	1	0
Aceraspis sp2	1	0	1	0	1	1	1	0	0	0	1	0	0	1	0
Bremiella pulchella	0	0	0	0	0	–	0	0	0	0	0	2	0	1	0
Bothromus bicolor	0	0	0	0	0	–	1	1	0	0	0	1	0	0	0
Bothromus minoris	0	0	0	0	0	–	1	1	0	0	0	1	0	0	0
Carria dreisbachi	0	0	0	1	–	–	0	0	0	0	0	1	0	0	0
Chorinaeus californicus	1	0	0	0	0	–	1	0	1	0	0	1	0	0	0
Chorinaeus cristator	1	0	0	0	0	–	1	0	1	0	0	1	0	0	0
Chorinaeus funebris	1	0	0	0	0	–	1	0	1	0	0	1	0	0	0
Chorinaeus subcarinatus	1	0	0	0	0	–	1	0	1	0	0	1	0	0	0
Colpotrochia cincta	1	0	0	1	–	–	0	0	1	0	0	2	0	1	0
Colpotrochia watanka	1	0	0	0	0	–	0	0	1	0	0	2	0	1	0
Colpotrochia sp	1	0	0	0	0	–	0	0	1	0	0	2	0	1	0
Cubus sp1	1	0	0	1	–	–	0	0	1	0	0	2	1	1	0
Cubus sp2	1	0	0	1	–	–	0	0	1	0	0	2	1	1	0
Drepanoctonus bifasciatus	0	0	0	0	0	–	0	0	0	0	0	1	0	0	0
Drepanoctomus sp	0	0	0	0	0	–	0	0	0	0	0	1	0	0	0
Exochus izbus	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Exochus mitratos	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Exochus spinalis	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Exochus tegularis	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Exochus sp	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Exochus sp6	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Exochus CNC1	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Finisterra rubra	0	0	0	1	–	–	0	0	1	0	0	2	0	1	0
Finisterra B5	0	0	0	1	–	–	0	0	1	0	0	2	0	1	0
Finisterra B9	0	0	0	1	–	–	0	0	1	0	0	2	0	1	0
Forrestopius judyae	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Forrestopius larryi	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Forrestopius pamelae	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Forrestopius AEIC4	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Forrrestopius CNC7	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Forrrestopius sp4	0	0	0	1	–	–	0	0	1	0	0	2	0	0	0
Hemimetopius angulitarsus	1	0	1	0	1	0	1	0	1	0	1	0	0	1	1
Hemimetopius sp	1	0	1	0	1	0	1	0	1	0	1	0	0	1	1
Huetzin acarinatus	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Hypsicera curvator	0	0	0	1	–	–	0	0	1	0	0	1	2	0	0
Hypsicera femoralis	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Hypsicera CNC1	0	0	0	0	0	–	0	0	1	0	0	1	0	0	0

Hypsicera 2	0	0	0	1	–	–	0	0	1	0	0	1	2	0	0
Hypsicera (Stethoncus) articus	0	0	0	1	–	–	0	0	1	0	0	1	2	0	0
Hypsicera (Stethoncus) AEIC1	0	0	0	1	–	–	0	0	1	0	0	1	2	0	0
Ischyrocnemis goesi	1	0	0	0	0	–	0	0	1	0	0	2	0	?	0
Jirajara yacambuensis	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Lapton femoralis	1	0	0	0	0	–	0	0	0	0	0	2	0	?	0
Leurus angustignathus	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Leurus cauriventris	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Leurus fascialis	0	0	0	1	–	–	0	0	1	0	0	2	0	0	0
Leurus xalifer	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Leurus MUSM2	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Leurus sp6	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Leurus A9	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Leurus A10	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Leurus AEIC3	0	0	0	1	–	–	0	0	1	0	0	2	0	0	0
Leurus AEIC4	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Macromalon montanum	0	0	0	1	–	–	0	0	1	0	0	2	0	0	0
Metopius dentatus	1	0	1	0	1	1	1	0	0	0	1	1	0	1	0
Metopius pollictorius	1	0	1	0	1	1	1	0	0	0	1	1	0	1	0
Ojuelus juachicus	1	0	?	1	–	–	0	0	1	0	0	1	0	1	0
Periope auscultator	0	0	0	1	–	–	0	0	0	0	0	1	0	0	0
Periope aethiops	0	0	0	1	–	–	0	0	0	0	0	1	0	0	0
Pseudometopius hagenii	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0
Sciron A17	0	0	0	1	–	–	0	0	0	0	0	1	0	0	0
Sciron sp	0	0	0	1	–	–	0	0	0	0	0	1	0	0	0
Scolomus borealis	1	0	?	1	–	–	0	0	0	0	0	2	0	0	0
Scolomus magellanicus	0	0	0	1	–	–	0	0	–	1	0	2	0	0	0
Scolomus viridis	0	0	0	1	–	–	0	0	–	1	0	2	0	0	0
Scolomus sp	1	0	0	?	?	?	?	0	0	0	0	2	0	0	0
Seticornuta albopilosa	1	0	0	1	–	–	1	0	1	0	0	1	0	1	0
Seticornuta cortesi	1	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Seticornuta terminalis	1	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Seticornuta Brazil	1	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Seticornuta Guadalcanal	1	0	0	1	–	–	1	0	1	0	0	1	0	1	0
Spudaeus indigus	1	0	0	1	–	–	1	0	0	0	0	1	0	1	0
Spudaeus scaber	1	0	0	1	–	–	1	0	0	0	0	1	0	1	0
Synosis clepsidra	0	1	0	1	–	–	1	0	1	0	0	1	0	0	0
Synosis sp	0	1	0	1	–	–	1	0	1	0	0	1	0	0	0
Triclistus cholo	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Triclistus emarginalus	1	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Triclistus occidentis	0	0	0	1	–	–	0	0	1	0	0	1	0	1	0
Trieces bicalcaratus	1	0	0	0	0	–	1	0	1	0	0	0	0	1	1
Trieces flavifrons	1	0	0	0	0	–	1	0	1	0	0	1	0	1	1
Trieces horisme	1	0	0	0	0	–	1	0	1	0	0	2	0	1	1
Trieces peruvianus	1	0	0	0	0	–	1	0	1	0	0	2	0	1	1
Trieces tyloides	1	0	0	0	0	–	1	0	1	0	0	2	0	1	1
Wira luisi	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Wira AEICE	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Wira AEICF	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Wira C5	0	0	0	1	–	–	0	0	1	0	0	1	0	0	0
Yanesha chorui	1	0	0	1	–	–	0	0	1	0	0	2	0	1	0

Continuing Appendix 2

Taxa	Characters														
	75	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**
Enicospilus flavoscutellatus	0	0	0	–	0	0	0	0	0	0	0	–	0	–	0
Aphanistes cachil	0	0	0	–	0	1	0	–	–	–	–	–	0	–	0
Mnioes lunatus	0	0	0	–	0	0	0	1	1	0	0	–	0	–	0
Cidaphus sp	1	0	0	–	0	1	0	0	0	1	0	–	1	3	0
Mesochorus sp	1	0	0	–	0	1	1	0	0	1	0	–	1	3	0
Alexeter innoxius	0	0	0	–	0	0	1	1	0	1	0	–	1	2	1
Euryproctus sp	0	0	0	–	0	0	1	1	0	1	0	–	0	–	0
Perilissus decoloratus	0	0	0	–	0	0	1	0	0	1	1	1	1	2	0
Phobetes sp	0	0	0	–	0	0	1	1	1	1	0	–	0	–	0
Xenoschesis limata	0	0	0	–	0	1	1	1	1	0	0	–	1	2	1
Neliopisthus sp	1	0	0	–	0	1	1	0	0	1	1	0	1	–	1
Aceraspis sp1	1	0	0	–	1	1	0	0	0	1	0	–	1	3	0
Aceraspis sp2	1	0	0	–	1	1	0	0	0	1	0	–	1	3	0
Bremiella pulchella	0	0	0	–	1	1	0	0	0	1	0	–	1	1	0
Bothromus bicolor	0	0	0	–	0	1	1	1	0	1	1	1	0	–	0
Bothromus minoris	0	0	0	–	0	1	1	1	0	1	1	1	0	–	0
Carria dreisbachi	1	0	1	0	0	1	1	1	0	1	0	–	1	2	0
Chorinaeus californicus	1	0	1	0	1	1	0	1	0	1	1	0	0	–	0
Chorinaeus cristator	1	0	1	0	1	1	0	1	0	1	1	0	0	–	0
Chorinaeus funebris	1	0	1	0	1	1	0	1	0	1	1	0	0	–	0
Chorinaeus subcarinatus	1	0	1	0	1	1	0	1	0	1	1	0	0	–	0
Colpotrochia cincta	1	0	0	–	0	1	0	1	1	1	0	–	0	–	0
Colpotrochia watanka	1	0	0	–	0	1	0	1	1	1	0	–	0	–	0
Colpotrochia sp	1	0	0	–	0	1	0	1	1	1	0	–	0	–	0
Cubus sp1	1	0	1	0	0	1	0	1	1	1	0	–	0	–	1
Cubus sp2	1	0	1	0	0	1	0	1	1	1	0	–	0	–	1
Drepanoctonus bifasciatus	0	0	0	–	0	1	0	1	0	0	0	–	0	–	0
Drepanoctomus sp	0	0	0	–	0	1	0	0	0	0	0	–	0	–	0
Exochus izbus	1	0	1	0	0	1	0	0	0	1	0	–	0	–	0
Exochus mitratos	1	0	1	0	0	1	0	0	0	1	0	–	0	–	0
Exochus spinalis	1	0	1	0	0	1	1	1	0	1	0	–	0	–	0
Exochus tegularis	1	0	1	0	0	1	0	0	0	1	0	–	0	–	0
Exochus sp	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Exochus sp6	1	0	1	0	0	1	0	0	0	1	0	–	0	–	0
Exochus CNC1	1	0	1	0	0	1	0	0	0	1	0	–	0	–	0
Finisterra rubra	1	0	0	–	0	1	0	1	0	1	1	1	1	2	0
Finisterra B5	0	0	0	–	0	1	0	1	0	1	1	1	1	2	0
Finisterra B9	0	0	0	–	0	1	0	1	0	1	1	1	1	2	0
Forrestopius judyae	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Forrestopius larryi	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Forrestopius pamelae	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Forrestopius AEIC4	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Forrrestopius CNC7	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Forrrestopius sp4	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Hemimetopius angulitarsus	1	1	0	–	1	1	0	1	0	1	1	0	0	–	0
Hemimetopius sp	1	1	0	–	1	1	0	1	0	1	1	0	0	–	0
Huetzin acarinatus	1	0	1	0	0	1	0	1	0	1	0	–	1	2	0
Hypsicera curvator	1	0	1	1	0	1	1	0	0	1	0	–	0	–	0
Hypsicera femoralis	1	0	1	1	0	1	0	0	0	1	0	–	0	–	0
Hypsicera CNC1	1	0	1	1	0	1	0	0	0	1	0	–	0	–	0

Hypsicera 2	1	0	1	1	0	1	1	1	0	1	0	–	0	–	0
Hypsicera (Stethoncus) articus	1	0	1	1	0	1	1	0	0	1	0	–	0	–	0
Hypsicera (Stethoncus) AEIC1	1	0	1	1	0	1	1	0	0	1	0	–	0	–	0
Ischyrocnemis goesi	0	0	0	–	0	1	0	1	0	1	0	–	1	2	0
Jirajara yacambuensis	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Lapton femoralis	0	0	0	–	0	0	0	0	1	1	0	–	0	–	0
Leurus angustignathus	1	0	1	0	0	1	0	1	0	1	1	1	1	2	0
Leurus cauriventris	1	0	1	0	0	1	0	1	0	1	1	1	0&1	2	0
Leurus fascialis	1	0	1	0	0	1	0	1	1	0	1	1	1	2	0
Leurus xalifer	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Leurus MUSM2	1	0	1	0	0	1	0	1	0	1	1	1	0	–	0
Leurus sp6	1	0	1	0	0	1	0	1	0	1	1	1	1	2	0
Leurus A9	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Leurus A10	1	0	1	0	0	1	0	1	0	1	0	–	0	–	0
Leurus AEIC3	1	0	1	0	0	1	0	1	0	0	1	1	1	2	0
Leurus AEIC4	1	0	1	0	0	1	0	1	0	1	1	1	1	2	0
Macromalon montanum	1	0	0	–	0	1	1	0	0	1	0	–	0	–	0
Metopius dentatus	0	0	0	–	0	1	0	1	1	1	0	–	1	1	1
Metopius pollictorius	0	0	0	–	0	1	0	0	0	1	0	–	1	1	1
Ojuelus juachicus	1	0	0	–	0	1	0	1	0	1	0	–	1	2	0
Periope auscultator	0	0	0	–	0	1	1	1	0	1	0	–	1	2	0
Periope aethiops	0	0	0	–	0	1	1	1	0	1	0	–	1	2	0
Pseudometopius hagenii	0	0	0	–	1	1	0	0	0	1	1	0	1	2	0
Sciron A17	1	0	1	0	0	1	1	1	0	1	0	–	1	2	0
Sciron sp	1	0	1	0	0	1	1	1	0	1	0	–	1	2	0
Scolomus borealis	1	0	0	–	0	1	1	0	0	1	1	0	1	3	0
Scolomus magellanicus	0	0	0	–	0	1	1	0	0	1	0	–	1	3	0
Scolomus viridis	0	0	0	–	0	1	1	0	0	1	1	0	1	3	0
Scolomus sp	1	0	0	–	0	1	1	0	0	1	1	0	1	3	0
Seticornuta albopilosa	0	0	1	0	1	1	0	1	0	1	1	0	1	2	0
Seticornuta cortesi	1	0	1	0	0	1	0	1	0	1	1	1	1	2	0
Seticornuta terminalis	1	0	1	0	0	1	0	1	0	1	1	0	1	2	0
Seticornuta Brazil	1	0	1	0	0	1	0	1	0	1	1	1	1	2	0
Seticornuta Guadalcanal	0	0	1	0	1	1	0	1	0	1	1	0	1	2	0
Spudaeus indigus	0	0	0	–	0	1	0	1	0	1	1	0	1	2	0
Spudaeus scaber	0	0	0	–	0	1	0	1	0	1	1	0	1	2	0
Synosis clepsidra	1	0	1	1	0	1	1	0	0	1	0	–	0	–	0
Synosis sp	1	0	1	1	0	1	1	0	0	1	0	–	0	–	0
Triclistus cholo	1	0	1	0	0	1	1	1	0	1	0	–	1	2	0
Triclistus emarginalus	1	0	1	0	0	1	1	0	0	1	0	–	1	2	0
Triclistus occidentis	1	0	1	0	0	1	1	0	0	1	0	–	1	2	0
Trieces bicalcaratus	1	1	1	0	1	1	0	1	0	1	1	0	0	–	0
Trieces flavifrons	1	1	1	0	1	1	0	1	0	1	1	0	0	–	0
Trieces horisme	1	1	1	0	1	1	0	1	0	1	1	0	0	–	0
Trieces peruvianus	1	1	1	0	1	1	0	1	0	1	1	0	0	–	0
Trieces tyloides	1	1	1	0	1	1	0	1	0	1	1	0	0	–	0
Wira luisi	1	0	0	–	0	1	1	1	0	1	0	–	0	–	0
Wira AEICE	1	0	1	0	0	1	1	1	0	1	0	–	0	–	0
Wira AEICF	1	0	1	0	0	1	1	1	0	1	0	–	0	–	0
Wira C5	1	0	0	–	0	1	1	1	0	1	0	–	0	–	0
Yanesha chorui	1	0	1	0	0	1	1	1	0	1	1	1	0	–	0

Continuing Appendix 2

Taxa	Characters														
	90	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**
Enicospilus flavoscutellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphanistes cachil	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1
Mnioes lunatus	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1
Cidaphus sp	0	1	2	0	0	1	1	1	0	0	0	0	0	0	1
Mesochorus sp	1	0	–	0	1	1	1	1	0	0	0	0	0	0	0
Alexeter innoxius	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0
Euryproctus sp	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0
Perilissus decoloratus	1	0	2	0	1	1	1	1	1	0	0	0	0	0	0
Phobetes sp	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0
Xenoschesis limata	1	0	0	0	1	1	1	1	1	0	0	0	0	0	1
Neliopisthus sp	1	0	0	0	1	1	1	1	0	0	0	0	0	0	2
Aceratapsis sp1	2	1	1	1	0	1	1	1	0	1	1	1	0	2	2
Aceratapsis sp2	2	1	1	1	0	1	1	1	0	1	1	1	0	2	?
Bremiella pulchella	2	0	1	0	1	1	1	1	0	0	1	0	0	0	0
Bothromus bicolor	1	0	0	0	0	1	1	1	0	1	1	1	0	0	0
Bothromus minoris	1	0	0	0	0	1	1	1	0	1	1	1	0	0	0
Carria dreisbachi	1	0	0	1	1	1	1	1	0	1	1	1	0	0	2
Chorinaeus californicus	1	0	0	0	0	1	1	1	0	1	1	1	0	0	0
Chorinaeus cristator	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0
Chorinaeus funebris	1	0	0	0	0	1	1	1	0	1	1	1	0	0	0
Chorinaeus subcarinatus	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0
Colpotrochia cincta	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1
Colpotrochia watanka	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1
Colpotrochia sp	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1
Cubus sp1	1	1	0	1	1	1	1	1	0	1	1	1	0	0	0
Cubus sp2	1	1	0	1	1	1	1	1	0	1	1	1	0	0	0
Drepanoctonus bifasciatus	2	1	0	1	1	1	?	1	0	1	1	0	0	0	2
Drepanoctomus sp	2	1	0	1	1	1	0	1	0	1	1	0	0	0	2
Exochus izbus	1	0	0	1	1	1	0	0	0	1	1	1	0	0	0
Exochus mitratos	1	1	0	1	1	1	0	0	0	1	1	1	0	0	0
Exochus spinalis	1	0	–	1	1	1	0	0	0	1	1	1	0	0	0
Exochus tegularis	1	0	0	1	1	1	0	0	0	1	1	1	0	0	0
Exochus sp	1	1	0	1	1	1	0	0	0	1	1	1	0	0	0
Exochus sp6	1	0	0	1	1	1	0	0	0	1	1	1	0	0	0
Exochus CNC1	1	1	0	1	1	1	0	0	0	1	1	1	0	0	0
Finisterra rubra	0	1	0	1	1	1	1	1	0	1	1	1	0	0	1
Finisterra B5	0	1	0	1	1	1	1	1	0	1	1	1	0	0	1
Finisterra B9	0	1	0	1	1	1	1	1	0	1	1	1	0	0	1
Forrestopius judyae	1	0	0	1	1	0	0	0	0	1	1	1	0	0	2
Forrestopius larryi	1	1	0	1	1	1	1	1	0	1	1	1	0	0	?
Forrestopius pamelae	1	0	0	1	1	0	0	0	0	1	1	1	0	0	2
Forrestopius AEIC4	1	0	0	1	1	0	0	0	0	1	1	1	0	0	2
Forrrestopius CNC7	1	0	0	1	1	0	0	0	0	1	1	1	0	0	2
Forrrestopius sp4	1	0	0	1	1	0	0	0	0	1	1	1	0	0	2
Hemimetopius angulitarsus	1	1	0	1	0	1	1	1	0	1	1	0	0	0	2
Hemimetopius sp	1	1	1	1	0	1	1	1	0	1	1	0	0	0	2
Huetzin acarinatus	1	0	0	1	1	1	1	1	0	1	1	1	0	0	2
Hypsicera curvator	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1
Hypsicera femoralis	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1
Hypsicera CNC1	1	0	0	1	1	0	0	0	0	1	1	1	0	0	1

Hypsicera 2	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1
Hypsicera (Stethoncus) articus	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1
Hypsicera (Stethoncus) AEIC1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1
Ischyrocnemis goesi	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0
Jirajara yacambuensis	1	0	0	1	1	1	1	1	0	1	1	1	0	0	0
Lapton femoralis	0	0	2	0	0	0	?	1	1	0	?	0	0	0	0
Leurus angustignathus	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus cauriventris	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus fascialis	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus xalifer	1	?	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus MUSM2	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus sp6	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus A9	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus A10	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus AEIC3	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Leurus AEIC4	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Macromalon montanum	1	0	0	0	1	1	1	1	0	1	1	1	0	0	1
Metopius dentatus	2	1	2	1	1	0	0	0	1	0	1	0	1	1	–
Metopius pollictorius	2	1	2	1	1	0	0	0	1	0	1	0	1	1	–
Ojuelus juachicus	?	?	0	1	1	?	?	?	?	1	1	1	0	0	2
Periope auscultator	2	0	0	0	1	1	1	1	0	1	1	0	0	0	0
Periope aethiops	2	1	0	0	1	1	1	1	0	1	1	0	0	0	0
Pseudometopius hagenii	2	1	1	0	0	1	1	1	0	0	1	1	0	0	2
Sciron A17	1	0	0	0	1	1	1	1	0	1	1	1	0	0	1
Sciron sp	1	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Scolomus borealis	?	?	0	1	1	?	?	?	0	1	1	1	0	0	2
Scolomus magellanicus	0	1	0	1	1	1	1	1	1	0	1	0	0	0	1
Scolomus viridis	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1
Scolomus sp	1	0	0	1	1	0	0	0	0	1	1	1	0	0	2
Seticornuta albopilosa	2	1	0	1	1	1	1	1	0	1	1	1	0	0	1
Seticornuta cortesi	1	1	0	1	1	1	1	1	0	1	1	1	0	0	2
Seticornuta terminalis	1	1	0	1	1	1	1	1	0	1	1	1	0	0	2
Seticornuta Brazil	1	1	0	1	1	1	1	1	0	1	1	1	0	0	2
Seticornuta Guadalcanal	2	1	0	1	1	1	1	1	0	1	1	1	0	0	1
Spudaeus indigus	2	1	1	1	1	1	1	1	0	0	1	1	0	0	2
Spudaeus scaber	2	1	1	1	1	1	1	1	0	0	1	1	0	0	2
Synosis clepsidra	1	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Synosis sp	1	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Triclistus cholo	1	0	0	1	1	1	1	1	0	1	1	1	0	0	2
Triclistus emarginalus	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Triclistus occidentis	1	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Trieces bicalcaratus	1	0	1	1	0	1	1	1	0	1	1	1	0	0	0
Trieces flavifrons	1	0	0	0	0	1	1	1	0	1	1	1	0	0	0
Trieces horisme	1	0	–	1	0	1	1	1	0	1	1	1	0	0	0
Trieces peruvianus	1	0	–	1	0	1	1	1	0	1	1	0	0	0	0
Trieces tyloides	1	0	0	1	0	1	1	1	0	1	1	1	0	0	0
Wira luisi	1	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Wira AEICE	1	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Wira AEICF	1	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Wira C5	1	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Yanesha chorui	1	0	0	1	1	1	1	1	0	1	1	1	0	0	2

Continuing Appendix 2

Taxa	Characters													
	105	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**
Enicospilus flavoscutellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphanistes cachil	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Mnioes lunatus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Cidaphus sp	0	0	1	0	0	0	0	1	1	0	0	0	0	0
Mesochorus sp	0	0	1	0	0	0	0	1	1	1	0	0	0	0
Alexeter innoxius	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Euryproctus sp	0	0	1	0	0	0	1	0	1	1	0	0	0	0
Perilissus decoloratus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Phobetes sp	0	0	1	0	0	0	1	0	1	1	0	0	0	0
Xenoschesis limata	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Neliopisthus sp	0	0	1	0	0	0	1	1	1	1	0	0	0	0
Aceratapsis sp1	1	1	–	0	0	0	1	2	1	1	1	1	0	0
Aceratapsis sp2	1	1	–	0	0	?	1	2	1	1	1	1	0	0
Bremiella pulchella	0	0	1	0	0	0	0	1	1	1	0	0	0	0
Bothromus bicolor	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Bothromus minoris	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Carria dreisbachi	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Chorinaeus californicus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Chorinaeus cristator	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Chorinaeus funebris	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Chorinaeus subcarinatus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Colpotrochia cincta	0	0	1	0	0	0	0	2	1	0	0	1	0	0
Colpotrochia watanka	0	0	1	0	0	0	0	2	1	0	0	0	0	0
Colpotrochia sp	0	0	1	0	0	0	0	2	1	0	0	0	0	0
Cubus sp1	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Cubus sp2	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Drepanoctonus bifasciatus	0	1	–	0	0	0	1	2	1	1	1	?	0	0
Drepanoctomus sp	0	1	–	0	0	0	1	2	1	1	1	1	0	0
Exochus izbus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Exochus mitratos	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Exochus spinalis	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Exochus tegularis	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Exochus sp	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Exochus sp6	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Exochus CNC1	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Finisterra rubra	0	0	1	0	0	1	1	2	1	1	0	0	0	0
Finisterra B5	0	0	1	0	0	1	1	2	1	1	0	0	0	0
Finisterra B9	0	0	1	0	0	1	1	2	1	1	0	0	0	0
Forrestopius judyae	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Forrestopius larryi	0	0	0	0	0	0	1	2	1	1	0	0	0	0
Forrestopius pamelae	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Forrestopius AEIC4	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Forrrestopius CNC7	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Forrrestopius sp4	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Hemimetopius angulitarsus	1	0	1	1	1	0	1	2	1	1	0	0	0	0
Hemimetopius sp	1	0	1	1	1	0	1	2	1	1	0	0	0	0
Huetzin acarinatus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Hypsicera curvator	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Hypsicera femoralis	0	0	1	0	0	0	1	2	1	1	0	0	0	0

Hypsicera CNC1	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Hypsicera 2	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Hypsicera (Stethoncus) articus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Hypsicera (Stethoncus) AEIC1	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Ischyrocnemis goesi	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Jirajara yacambuensis	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Lapton femoralis	0	1	–	0	0	?	1	2	1	1	0	0	0	0
Leurus angustignathus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Leurus cauriventris	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Leurus fascialis	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Leurus xalifer	0	?	?	0	0	0	1	2	1	1	0	0	0	0
Leurus MUSM2	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Leurus sp6	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Leurus A9	0	0	0	0	0	0	1	2	1	1	0	0	0	0
Leurus A10	0	0	0	0	0	0	1	2	1	1	0	0	0	0
Leurus AEIC3	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Leurus AEIC4	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Macromalon montanum	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Metopius dentatus	1	1	–	0	0	0	1	2	1	1	1	1	1	1
Metopius pollictorius	1	1	–	0	0	0	1	2	1	1	1	1	1	1
Ojuelus juachicus	0	?	?	0	0	0	1	2	1	1	0	0	0	0
Periope auscultator	0	1	–	0	0	0	0	2	1	1	0	0	0	0
Periope aethiops	0	1	–	0	0	0	0	2	1	1	0	0	0	0
Pseudometopius hagenii	0	1	–	0	0	0	1	2	1	1	1	1	0	0
Sciron A17	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Sciron sp	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Scolomus borealis	0	?	?	0	0	1	1	2	1	1	0	0	0	0
Scolomus magellanicus	0	0	1	0	0	1	1	1	1	1	0	0	0	0
Scolomus viridis	0	0	1	0	0	?	1	1	1	1	0	0	0	0
Scolomus sp	0	0	1	0	0	1	1	2	1	1	0	0	0	0
Seticornuta albopilosa	0	1	–	0	0	0	1	2	1	1	0	0	1	0
Seticornuta cortesi	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Seticornuta terminalis	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Seticornuta Brazil	0	1	–	0	0	0	1	2	1	1	0	0	0	0
Seticornuta Guadalcanal	0	1	–	0	0	?	1	2	1	1	0	0	1	0
Spudaeus indigus	1	1	–	0	0	0	1	2	1	1	1	1	0	0
Spudaeus scaber	1	1	–	0	0	0	1	2	1	1	1	1	0	0
Synosis clepsidra	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Synosis sp	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Triclistus cholo	0	0	1	0	0	1	1	2	1	1	0	0	0	0
Triclistus emarginalus	0	0	1	0	0	1	1	2	1	1	0	0	0	0
Triclistus occidentis	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Trieces bicalcaratus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Trieces flavifrons	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Trieces horisme	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Trieces peruvianus	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Trieces tyloides	0	0	1	0	0	0	1	2	1	1	0	0	0	0
Wira luisi	0	0	0	0	0	?	1	2	1	1	0	0	0	0
Wira AEICE	0	0	1	0	0	?	1	2	1	1	0	0	0	0
Wira AEICF	0	0	1	0	0	?	1	2	1	1	0	0	0	0
Wira C5	0	0	0	0	0	?	1	2	1	1	0	0	0	0
Yanesha chorui	0	1	–	0	0	0	1	2	1	1	0	0	0	0

Continuing Appendix 2

Taxa	Characters													
	119	120	121	122	123	124	125	126	127	128	129	130	131	132
Enicospilus flavoscutellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphanistes cachil	1	–	0	0	0	0	0	0	0	0	0	0	0	0
Mnioes lunatus	0	1	0	0	0	0	0	0	0	2	2	0	0	0
Cidaphus sp	1	–	0	0	0	0	0	1	0	1	1	0	0	0
Mesochorus sp	0	1	0	0	0	0	0	1	0	1	1	0	0	0
Alexeter innoxius	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Euryproctus sp	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Perilissus decoloratus	1	–	0	0	0	0	0	1	0	1	2	0	0	0
Phobetes sp	0	1	0	0	0	0	0	1	0	1	2	0	0	0
Xenoschesis limata	0	1	0	0	0	0	0	1	0	1	1	0	0	0
Neliopisthus sp	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Aceratapsis sp1	0	1	0	2	1	1	0	1	0	2	2	0	1	0
Aceratapsis sp2	0	1	0	2	1	1	0	1	0	2	2	0	1	0
Bremiella pulchella	1	1	0	0	0	0	0	1	0	2	?	0	0	?
Bothromus bicolor	0	1	0	0	0	1	1	1	0	2	?	0	0	0
Bothromus minoris	0	1	0	0	0	1	1	1	0	2	2	0	0	0
Carria dreisbachi	1	1	0	0	0	0	0	1	0	2	2	0	0	0
Chorinaeus californicus	1	–	0	2	0	2	1	1	0	2	2	0	1	0
Chorinaeus cristator	1	–	0	2	0	2	1	1	0	2	2	0	1	0
Chorinaeus funebris	1	–	0	2	0	2	1	1	0	2	2	0	1	0
Chorinaeus subcarinatus	1	–	0	2	0	2	1	1	0	2	2	0	1	0
Colpotrochia cincta	0	1	0	1	0	0	0	1	0	2	2	0	0	0
Colpotrochia watanka	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Colpotrochia sp	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Cubus sp1	1	–	0	0	0	0	0	1	0	1	2	0	0	0
Cubus sp2	1	–	0	0	0	0	0	1	0	1	?	0	0	0
Drepanoctonus bifasciatus	0	1	0	0	1	1	0	1	0	2	2	1	0	0
Drepanoctomus sp	0	1	0	0	1	1	0	1	0	2	2	1	0	0
Exochus izbus	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Exochus mitratos	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Exochus spinalis	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Exochus tegularis	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Exochus sp	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Exochus sp6	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Exochus CNC1	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Finisterra rubra	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Finisterra B5	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Finisterra B9	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Forrestopius judyae	1	–	0	0	0	0	0	1	0	2	?	1	0	0
Forrestopius larryi	1	–	0	0	0	0	0	1	0	2	2	1	0	1
Forrestopius pamelae	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Forrestopius AEIC4	1	–	0	0	0	0	0	1	0	2	?	1	0	0
Forrrestopius CNC7	1	–	0	0	0	0	0	1	0	2	?	1	0	0
Forrrestopius sp4	1	1	0	0	0	0	0	1	0	2	?	0	0	0
Hemimetopius angulitarsus	1	–	0	2	0	2	1	1	0	2	2	0	1	0
Hemimetopius sp	1	–	0	2	0	2	1	1	0	2	2	0	1	0
Huetzin acarinatus	0	1	0	0	0	0	0	1	0	2	2	0	0	0
Hypsicera curvator	0	1	0	0	0	0	0	1	0	2	?	1	0	0
Hypsicera femoralis	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Hypsicera CNC1	1	–	0	0	0	0	0	1	0	2	2	1	0	0

Hypsicera 2	0	1	0	0	0	0	0	1	0	2	?	1	0	0
Hypsicera (Stethoncus) articus	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Hypsicera (Stethoncus) AEIC1	1	–	0	0	0	0	0	1	0	2	?	1	0	0
Ischyrocnemis goesi	0	1	0	1	0	0	0	1	0	1	?	2	0	0
Jirajara yacambuensis	0	1	0	0	0	0	0	1	0	2	2	1	0	0
Lapton femoralis	0	1	0	0	0	0	0	1	0	1	1	2	0	?
Leurus angustignathus	0	1	0	0	0	0	0	1	0	2	2	1	0	0
Leurus cauriventris	0	1	0	0	0	0	0	1	0	2	2	1	0	0
Leurus fascialis	1	–	0	0	0	0	0	1	0	2	?	1	0	0
Leurus xalifer	1	–	0	0	0	0	0	1	0	2	?	1	0	0
Leurus MUSM2	0	1	0	?	0	0	0	1	?	?	?	1	0	0
Leurus sp6	0	1	0	0	0	0	0	1	0	2	2	1	0	0
Leurus A9	1	–	0	1	0	0	0	1	0	2	2	1	0	1
Leurus A10	1	–	0	1	0	0	0	1	0	2	2	1	0	1
Leurus AEIC3	1	–	0	0	0	0	0	1	0	2	?	1	0	0
Leurus AEIC4	0	1	0	0	0	0	0	1	0	2	?	1	0	0
Macromalon montanum	0	1	0	0	0	0	0	1	0	2	2	1	0	0
Metopius dentatus	0	1	1	1	1	0	0	0	0	2	2	1	0	0
Metopius pollictorius	0	1	1	1	1	0	0	0	0	2	2	1	0	0
Ojuelus juachicus	0	1	0	0	0	0	0	1	0	2	?	1	0	0
Periope auscultator	0	1	0	0	0	1	0	0	0	2	2	1	0	0
Periope aethiops	0	1	0	0	0	1	0	1	0	2	2	1	0	0
Pseudometopius hagenii	0	0	0	2	1	1	0	1	0	2	2	1	1	0
Sciron A17	1	–	0	0	0	0	0	1	0	2	2	0	0	0
Sciron sp	1	–	0	0	0	0	0	1	0	2	2	0	0	0
Scolomus borealis	?	?	0	0	0	0	0	1	0	2	?	0	0	0
Scolomus magellanicus	0	1	0	0	0	0	0	0	0	1	2	0	0	0
Scolomus viridis	0	1	0	0	0	0	0	?	0	?	2	0	0	?
Scolomus sp	?	?	0	0	0	0	0	1	0	2	?	0	0	0
Seticornuta albopilosa	0	1	0	1	0	0	0	0	0	2	2	1	0	0
Seticornuta cortesi	0	1	0	1	0	0	0	1	0	2	?	1	0	0
Seticornuta terminalis	0	1	0	1	0	0	0	1	0	2	2	1	0	0
Seticornuta Brazil	0	1	0	1	0	0	0	1	0	2	2	1	0	0
Seticornuta Guadalcanal	0	1	0	1	0	0	0	?	0	?	2	1	0	?
Spudaeus indigus	0	0	0	0	0	1	1	1	0	2	2	1	0	0
Spudaeus scaber	0	0	0	0	0	1	1	1	0	2	2	1	0	0
Synosis clepsidra	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Synosis sp	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Triclistus cholo	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Triclistus emarginalus	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Triclistus occidentis	1	–	0	0	0	0	0	1	0	2	2	1	0	0
Trieces bicalcaratus	1	–	0	2	0	2	2	1	1	2	2	0	1	0
Trieces flavifrons	1	–	0	2	0	2	2	1	1	2	2	0	1	0
Trieces horisme	1	–	0	2	0	2	2	1	1	2	2	0	1	0
Trieces peruvianus	1	–	0	2	0	2	2	1	1	2	2	0	1	0
Trieces tyloides	1	–	0	2	0	2	2	1	1	2	2	0	1	0
Wira luisi	0	1	0	0	0	0	0	?	0	?	2	1	0	?
Wira AEICE	0	1	0	0	0	0	0	?	0	?	2	1	0	?
Wira AEICF	0	1	0	0	0	0	0	?	0	?	2	1	0	?
Wira C5	0	1	0	0	0	0	0	?	0	?	2	1	0	?
Yanesha chorui	0	1	0	0	0	0	0	1	0	2	?	1	0	0

Continuing Appendix 2

Taxa	Characters													
	133	134	135	136	137	138	139	140	141	142	143	144	145	146
Enicospilus flavoscutellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphanistes cachil	0	0	0	0	2	1	0	1	0	1	2	0	0	0
Mnioes lunatus	0	0	1	0	2	1	0	0	0	0	1	0	0	0
Cidaphus sp	1	0	1	0	1	1	2	1	–	–	1	1	0	0
Mesochorus sp	1	0	1	0	1	1	2	1	–	–	1	1	0	0
Alexeter innoxius	0	1	1	0	0	1	1	1	0	0	1	1	0	0
Euryproctus sp	0	0	1	0	0	1	1	1	0	0	1	1	0	0
Perilissus decoloratus	0	0	1	0	0	1	1	1	0	0	1	1	0	0
Phobetes sp	0	0	1	0	0	1	0	1	0	0	1	1	0	0
Xenoschesis limata	0	0	1	0	0	1	1	1	0	0	1	1	0	0
Neliopisthus sp	0	1	1	0	2	1	1	1	0	0	1	1	0	0
Aceraspis sp1	0	?	?	?	?	?	0	?	?	0	?	0	0	?
Aceraspis sp2	0	0	0	?	?	?	0	?	0	0	?	0	0	?
Bremiella pulchella	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bothromus bicolor	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Bothromus minoris	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Carria dreisbachi	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Chorinaeus californicus	0	0	1	1	1	1	0	0	0	0	1	0	0	1
Chorinaeus cristator	0	0	1	1	1	1	0	0	0	0	1	0	0	1
Chorinaeus funebris	0	0	1	1	1	1	0	0	0	0	1	0	0	0
Chorinaeus subcarinatus	0	0	1	1	1	1	0	0	0	0	1	0	0	0
Colpotrochia cincta	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Colpotrochia watanka	0	0	0	1	1	1	0	0	0	0	2	0	0	0
Colpotrochia sp	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Cubus sp1	0	0	1	1	1	1	0	0	0	1	2	0	0	0
Cubus sp2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Drepanoctonus bifasciatus	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Drepanoctomus sp	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Exochus izbus	0	0	0	1	1	1	0	0	0	0	2	?	0	1
Exochus mitratos	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Exochus spinalis	0	0	1	1	1	1	0	0	0	0	2	1	0	1
Exochus tegularis	0	0	0	1	1	1	0	0	0	0	2	1	0	1
Exochus sp	0	0	1	1	1	1	0	0	0	0	2	1	0	1
Exochus sp6	0	0	0	1	1	1	0	0	0	0	2	1	0	1
Exochus CNC1	0	0	1	1	1	1	0	0	0	0	2	1	0	1
Finisterra rubra	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Finisterra B5	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Finisterra B9	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Forrestopius judyae	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Forrestopius larryi	0	?	?	?	?	?	0	0	0	0	2	?	?	?
Forrestopius pamelae	1	?	?	?	?	?	0	0	1	0	2	?	?	?
Forrestopius AEIC4	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Forrrestopius CNC7	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Forrrestopius sp4	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Hemimetopius angulitarsus	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Hemimetopius sp	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Huetzin acarinatus	1	0	1	?	1	1	0	0	?	0	2	1	0	0
Hypsicera curvator	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Hypsicera femoralis	0	0	1	1	1	1	0	0	0	0	2	1	0	1
Hypsicera CNC1	0	0	1	1	1	1	0	0	0	0	2	1	0	1

Hypsicera 2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Hypsicera (Stethoncus) articus	0	0	1	1	1	1	0	0	0	0	2	1	0	1
Hypsicera (Stethoncus) AEIC1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Ischyrocnemis goesi	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Jirajara yacambuensis	0	0	1	?	?	1	0	0	?	0	2	1	0	0
Lapton femoralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Leurus angustignathus	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Leurus cauriventris	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Leurus fascialis	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Leurus xalifer	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Leurus MUSM2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Leurus sp6	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Leurus A9	1	0	1	1	1	1	0	0	0	0	2	1	0	0
Leurus A10	1	0	1	1	1	1	0	0	0	0	2	1	0	0
Leurus AEIC3	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Leurus AEIC4	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Macromalon montanum	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Metopius dentatus	0	0	0	1	1	1	1	0	0	0	1	1	0	0
Metopius pollictorius	0	0	0	1	1	1	1	0	0	0	1	1	0	0
Ojuelus juachicus	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Periope auscultator	0	0	0	?	?	?	0	?	0	0	2	?	?	?
Periope aethiops	0	0	0	1	1	0	0	0	0	0	2	0	0	0
Pseudometopius hagenii	0	0	0	1	1	1	0	0	0	1	1	1	0	0
Sciron A17	0	0	1	1	1	1	0	0	0	0	2	1	1	0
Sciron sp	0	0	1	1	1	1	0	0	0	0	2	1	1	0
Scolomus borealis	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Scolomus magellanicus	0	0	0	1	1	1	0	0	0	0	2	1	0	1
Scolomus viridis	?	0	0	?	?	?	0	0	0	0	2	1	0	1
Scolomus sp	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Seticornuta albopilosa	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Seticornuta cortesi	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Seticornuta terminalis	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Seticornuta Brazil	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Seticornuta Guadalcanal	?	0	1	1	1	1	0	0	0	0	2	1	0	0
Spudaeus indigus	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Spudaeus scaber	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Synosis clepsidra	0	0	1	1	1	1	0	0	0	0	2	1	0	1
Synosis sp	0	0	1	1	1	1	0	0	0	0	2	1	0	1
Triclistus cholo	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Triclistus emarginalus	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Triclistus occidentis	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Trieces bicalcaratus	0	0	1	1	1	1	0	0	0	0	2	0	0	1
Trieces flavifrons	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Trieces horisme	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Trieces peruvianus	0	0	1	1	1	1	0	0	0	0	2	0	0	0
Trieces tyloides	0	0	1	1	1	1	0	0	0	0	2	1	0	0
Wira luisi	?	0	1	1	1	1	0	0	1	0	2	1	0	0
Wira AEICE	?	0	1	1	1	1	0	0	?	?	2	1	0	0
Wira AEICF	?	0	1	?	?	?	0	0	?	?	2	1	0	0
Wira C5	?	0	1	1	1	1	0	0	1	0	2	1	0	0
Yanesha chorui	0	?	?	?	?	?	?	?	?	?	?	?	?	?

Continuing Appendix 2

Taxa	Characters													
	147	**148**	**149**	**150**	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**
Enicospilus flavoscutellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	–
Aphanistes cachil	0	0	0	0	0	0	0	0	0	0	0	0	0	–
Mnioes lunatus	1	1	1	0	0	0	0	0	0	1	0	1	2	–
Cidaphus sp	1	1	2	0	1	0	0	0	0	1	1	3	2	–
Mesochorus sp	1	1	2	0	1	0	0	0	0	0	1	3	2	–
Alexeter innoxius	1	0	1	0	1	0	0	0	1	1	1	2	0	–
Euryproctus sp	1	1	0	0	1	0	0	0	1	1	0	0	2	–
Perilissus decoloratus	1	0	1	0	1	0	0	0	1	1	1	0	0	–
Phobetes sp	1	1	1	0	1	0	0	0	1	1	1	0	0	–
Xenoschesis limata	1	1	1	0	1	0	0	1	1	1	0	2	0	–
Neliopisthus sp	1	1	1	0	1	0	0	0	0	0	1	0	0	–
Aceraspis sp1	?	?	?	?	0	0	?	0	0	0	1	0	0	–
Aceraspis sp2	?	?	?	?	0	0	?	?	?	?	?	?	?	?
Bremiella pulchella	?	?	?	?	?	?	?	?	?	?	?	?	0	–
Bothromus bicolor	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Bothromus minoris	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Carria dreisbachi	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Chorinaeus californicus	1	1	0	0	2	1	0	0	0	0	0	0	2	–
Chorinaeus cristator	1	1	0	0	2	0	0	0	0	0	1	0	2	–
Chorinaeus funebris	1	1	1	0	2	0	0	0	0	0	0	0	2	–
Chorinaeus subcarinatus	1	1	0	0	2	0	0	0	0	0	1	0	0	–
Colpotrochia cincta	1	1	0	1	0	0	1	0	1	1	1	1	1	1
Colpotrochia watanka	1	1	0	1	0	0	1	0	1	1	1	1	1	0
Colpotrochia sp	1	1	0	1	0	0	1	0	1	1	1	1	1	0
Cubus sp1	1	1	0	0	0	0	0	1	1	1	1	1	1	1
Cubus sp2	?	?	?	?	?	?	?	1	1	1	1	1	1	1
Drepanoctonus bifasciatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Drepanoctomus sp	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Exochus izbus	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Exochus mitratos	1	1	0	0	0	0	0	0	0	0	0	0	0	–
Exochus spinalis	1	1	0	1	0	0	0	0	0	0	1	0	0	–
Exochus tegularis	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Exochus sp	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Exochus sp6	1	1	3	1	0	0	0	0	0	0	1	0	0	–
Exochus CNC1	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Finisterra rubra	1	1	1	1	0	0	0	1	1	1	1	1	1	1
Finisterra B5	1	1	1	1	0	0	0	1	1	1	1	1	1	1
Finisterra B9	1	1	1	1	0	0	0	1	1	1	1	1	1	1
Forrestopius judyae	?	?	?	?	?	?	?	?	?	?	?	?	2	–
Forrestopius larryi	?	?	?	?	?	?	?	?	?	?	?	?	0	–
Forrestopius pamelae	?	?	?	?	?	?	?	?	?	?	?	?	0	–
Forrestopius AEIC4	?	?	?	?	?	?	?	0	0	0	1	0	2	–
Forrrestopius CNC7	?	?	?	?	?	?	?	0	0	0	1	0	2	–
Forrrestopius sp4	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Hemimetopius angulitarsus	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Hemimetopius sp	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Huetzin acarinatus	1	?	?	?	?	?	?	0	0	0	1	0	0	–
Hypsicera curvator	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Hypsicera femoralis	1	1	0	0	0	0	0	0	0	1	1	0	0	–
Hypsicera CNC1	1	1	0	0	0	0	0	0	0	0	1	0	0	–

Hypsicera 2	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Hypsicera (Stethoncus) articus	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Hypsicera (Stethoncus) AEIC1	?	?	?	?	?	?	?	0	0	?	?	?	0	–
Ischyrocnemis goesi	?	?	?	?	?	?	?	?	?	?	1	?	0	–
Jirajara yacambuensis	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Lapton femoralis	?	?	?	?	?	?	?	?	?	?	?	?	0	–
Leurus angustignathus	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Leurus cauriventris	1	1	0	0	0	1	0	0	0	0	1	0	0	–
Leurus fascialis	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Leurus xalifer	?	?	?	?	?	?	?	?	?	0	?	?	0	–
Leurus MUSM2	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Leurus sp6	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Leurus A9	1	1	0	0	0	0	0	0	0	0	0	0	2	–
Leurus A10	1	1	0	0	0	0	0	0	0	0	0	0	0	–
Leurus AEIC3	?	?	?	?	?	?	?	0	0	0	?	?	0	–
Leurus AEIC4	?	?	?	?	?	?	?	0	0	0	1	?	0	–
Macromalon montanum	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Metopius dentatus	1	1	0	0	2	0	0	0	0	0	0	0	0	–
Metopius pollictorius	1	1	2	0	2	0	0	0	0	0	0	0	0	–
Ojuelus juachicus	?	?	?	?	?	?	?	?	1	1	?	?	1	1
Periope auscultator	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Periope aethiops	1	1	0	0	0	0	0	0	0	1	0	0	2	–
Pseudometopius hagenii	1	1	2	0	0	0	0	0	0	0	1	0	2	–
Sciron A17	1	1	1	0	0	0	0	0	0	0	1	0	0	–
Sciron sp	1	1	1	1	0	0	0	0	0	0	1	0	0	–
Scolomus borealis	?	?	?	?	?	?	?	?	?	?	?	?	2	–
Scolomus magellanicus	1	0	1	0	1	0	0	1	1	1	1	1	1	2
Scolomus viridis	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Scolomus sp	?	?	?	?	?	?	?	?	?	?	?	?	2	–
Seticornuta albopilosa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Seticornuta cortesi	?	?	?	?	?	?	?	0	0	0	1	0	0	–
Seticornuta terminalis	1	1	0	0	0	2	0	0	0	0	1	0	0	–
Seticornuta Brazil	1	1	0	0	0	2	0	0	0	0	0	0	0	–
Seticornuta Guadalcanal	1	1	0	1	0	2	0	?	?	?	?	?	?	?
Spudaeus indigus	1	1	1	0	0	0	0	0	0	0	1	0	2	–
Spudaeus scaber	1	1	1	0	0	0	0	0	0	0	1	0	2	–
Synosis clepsidra	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Synosis sp	1	?	?	0	0	0	?	0	0	0	1	0	0	–
Triclistus cholo	1	1	0	1	0	0	0	1	1	1	1	1	1	1
Triclistus emarginalus	1	1	1	1	0	0	0	1	1	1	1	1	1	1
Triclistus occidentis	1	1	1	1	0	0	0	1	1	1	1	1	1	1
Trieces bicalcaratus	1	1	0	0	0	0	0	0	0	0	1	0	0	–
Trieces flavifrons	1	1	0	0	2	0	0	0	0	0	1	0	0	–
Trieces horisme	1	1	1	0	0	0	0	0	0	0	1	0	0	–
Trieces peruvianus	1	1	0	0	2	0	0	0	0	0	1	0	0	–
Trieces tyloides	1	1	0	0	2	0	0	0	0	0	1	0	0	–
Wira luisi	1	?	?	1	0	1	?	?	?	?	?	?	?	?
Wira AEICE	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Wira AEICF	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Wira C5	1	1	0	1	0	0	0	?	?	?	?	?	?	?
Yanesha chorui	?	?	?	?	?	?	?	0	0	0	0	0	0	–

Continuing Appendix 2

Taxa	Characters														
	161	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**	**171**	**172**	**173**	**174**	**175**
Enicospilus flavoscutellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphanistes cachil	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Mnioes lunatus	1	0	0	0	0	0	0	1	2	1	0	0	0	0	0
Cidaphus sp	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Mesochorus sp	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Alexeter innoxius	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Euryproctus sp	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Perilissus decoloratus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Phobetes sp	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Xenoschesis limata	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Neliopisthus sp	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Aceratapsis sp1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0
Aceratapsis sp2	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Bremiella pulchella	0	0	0	?	?	?	0	?	0	?	?	?	?	?	?
Bothromus bicolor	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Bothromus minoris	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Carria dreisbachi	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Chorinaeus californicus	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Chorinaeus cristator	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Chorinaeus funebris	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Chorinaeus subcarinatus	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Colpotrochia cincta	–	1	0	1	0	0	0	0	0	1	0	0	0	0	1
Colpotrochia watanka	–	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Colpotrochia sp	–	1	0	1	0	0	0	0	0	1	0	0	0	0	1
Cubus sp1	–	1	0	1	1	0	0	0	0	1	0	1	0	0	0
Cubus sp2	–	1	0	?	?	0	0	?	0	?	?	1	0	0	0
Drepanoctonus bifasciatus	?	?	1	?	?	?	?	?	0	?	?	?	?	?	?
Drepanoctomus sp	0	0	1	?	?	?	0	0	0	0	1	0	?	?	?
Exochus izbus	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Exochus mitratos	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Exochus spinalis	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Exochus tegularis	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Exochus sp	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Exochus sp6	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Exochus CNC1	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Finisterra rubra	–	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Finisterra B5	–	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Finisterra B9	–	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Forrestopius judyae	?	0	0	?	?	0	0	?	0	?	?	0	?	?	?
Forrestopius larryi	0	0	0	?	?	0	0	?	0	?	?	0	?	0	0
Forrestopius pamelae	?	0	0	?	?	0	0	?	0	?	?	0	?	?	?
Forrestopius AEIC4	0	0	0	?	?	0	0	?	0	?	?	0	?	0	0
Forrrestopius CNC7	0	0	0	?	?	0	0	?	0	?	?	0	?	0	0
Forrrestopius sp4	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Hemimetopius angulitarsus	0	0	1	1	2	1	1	0	0	1	1	0	0	0	0
Hemimetopius sp	0	0	1	?	?	1	1	?	0	?	?	0	0	0	0
Huetzin acarinatus	0	0	0	?	?	0	0	?	0	?	?	0	?	0	0
Hypsicera curvator	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Hypsicera femoralis	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Hypsicera CNC1	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0

Hypsicera 2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Hypsicera (Stethoncus) articus	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Hypsicera (Stethoncus) AEIC1	0	0	0	?	?	0	0	?	0	?	?	0	0	0	0
Ischyrocnemis goesi	0	0	0	0	?	?	0	?	0	?	?	0	?	?	?
Jirajara yacambuensis	0	0	0	?	?	0	0	?	0	?	?	0	?	0	0
Lapton femoralis	?	0	0	?	?	?	0	?	0	?	?	?	?	?	?
Leurus angustignathus	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Leurus cauriventris	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Leurus fascialis	0	0	0	?	?	0	0	?	0	1	1	0	0	0	0
Leurus xalifer	0	0	0	?	?	0	0	?	0	?	?	0	?	0	0
Leurus MUSM2	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Leurus sp6	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Leurus A9	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Leurus A10	0	0	0	1	0	0	0	?	0	1	1	0	0	0	0
Leurus AEIC3	0	0	0	?	?	0	0	?	0	?	?	0	0	0	0
Leurus AEIC4	0	0	0	?	?	0	0	?	0	?	?	0	0	0	0
Macromalon montanum	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Metopius dentatus	0	0	0	1	1	1	0	0	0	1	1	0	1	0	0
Metopius pollictorius	0	0	0	1	1	1	0	0	0	1	1	0	1	0	0
Ojuelus juachicus	–	1	0	?	?	0	0	?	0	?	?	?	?	?	?
Periope auscultator	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Periope aethiops	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Pseudometopius hagenii	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0
Sciron A17	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Sciron sp	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Scolomus borealis	0	0	0	?	?	?	0	?	0	?	?	?	?	?	?
Scolomus magellanicus	–	0	0	1	0	0	0	?	0	1	1	1	0	0	0
Scolomus viridis	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Scolomus sp	0	0	0	?	?	?	0	?	0	?	?	?	?	?	?
Seticornuta albopilosa	?	0	0	?	?	0	0	?	0	1	1	0	?	0	0
Seticornuta cortesi	0	0	0	?	?	0	0	?	0	1	1	0	0	0	0
Seticornuta terminalis	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Seticornuta Brazil	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Seticornuta Guadalcanal	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?
Spudaeus indigus	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0
Spudaeus scaber	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0
Synosis clepsidra	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Synosis sp	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Triclistus cholo	–	1	0	0	0	0	0	0	0	?	0	1	0	0	0
Triclistus emarginalus	–	1	0	0	0	0	0	0	0	?	0	1	0	0	0
Triclistus occidentis	–	1	0	0	0	0	0	0	0	?	0	1	0	0	0
Trieces bicalcaratus	0	0	0	1	2	0	0	?	0	?	?	0	0	0	0
Trieces flavifrons	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Trieces horisme	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Trieces peruvianus	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0
Trieces tyloides	0	0	0	1	2	0	0	0	0	1	1	0	0	0	0
Wira luisi	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Wira AEICE	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Wira AEICF	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Wira C5	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Yanesha chorui	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0

Appendix 3. Consistency index and Retention index per character; meso= mesosoma; meta = metasoma; N=non sex related; L = tree length; CI = consistency index; RI = retention index.

Character	Sex	Tagma	L	CI	RI
0	N	head	2	50	90
1	N	head	2	50	92
2	F	head	9	99	56
3	M	head	4	50	71
4	F	head	1	100	100
5	N	head	4	50	33
6	N	head	10	20	50
7	N	head	1	100	100
8	N	head	12	25	70
9	N	head	2	50	97
10	N	head	1	100	100
11	N	head	1	100	100
12	N	head	4	25	88
13	N	head	1	100	100
14	N	head	1	100	100
15	N	head	2	50	93
16	N	head	2	50	83
17	F	head	2	50	75
18	M	head	1	100	100
19	F	head	3	33	50
20	M	head	1	100	100
21	F	head	2	50	50
22	N	head	4	25	72
23	N	head	9	11	52
24	N	head	3	33	84
25	N	head	2	50	80
26	N	head	1	100	100
27	N	head	1	100	100
28	N	head	1	100	100
29	N	head	11	18	80
30	N	head	2	50	75
31	N	head	1	100	100
32	N	head	2	50	75
33	N	head	3	33	86
34	N	head	4	25	85
35	N	head	3	66	87
36	N	head	1	100	100
37	N	head	1	100	100
38	N	head	3	33	50
39	N	head	3	33	90
40	N	head	12	25	76
41	N	head	1	100	100
42	N	head	1	100	100
43	N	head	1	100	100

Character	Sex	Tagma	L	CI	RI
44	N	head	2	50	75
45	N	meso	1	100	100
46	N	meso	12	8	75
47	N	meso	1	100	100
48	N	meso	1	100	100
49	N	meso	2	50	95
50	N	meso	6	16	82
51	N	meso	5	20	75
52	N	meso	4	25	81
53	N	meso	9	22	66
54	N	meso	4	50	80
55	N	meso	1	100	100
56	N	meso	1	100	100
57	N	meso	2	50	92
58	N	meso	1	100	100
59	N	meso	5	20	66
60	N	meso	8	12	78
61	N	meso	1	100	100
62	N	meso	2	50	83
63	N	meso	7	14	76
64	N	meso	2	50	80
65	N	meso	1	100	100
66	N	meso	7	14	76
67	N	meso	1	100	100
68	N	meso	8	12	74
69	N	meso	1	100	100
70	N	meso	2	50	80
71	N	meso	16	12	58
72	N	meso	1	100	100
73	N	meso	7	14	83
74	N	meso	1	100	100
75	N	meso	7	14	77
76	N	meso	1	100	100
77	N	meso	7	14	85
78	N	meso	2	50	85
79	N	meso	5	20	75
80	N	meso	5	20	33
81	N	meso	12	8	66
82	N	meso	12	8	63
83	N	meso	6	16	50
84	N	meso	4	25	50
85	N	meso	10	10	75
86	N	meso	5	20	73
87	N	meso	13	7	70

Continuing Apendex 3

Character	Sex	Tagma	length	CI	RI
88	N	meso	5	40	66
89	N	meso	5	20	33
90	N	meso	8	25	68
91	N	meso	13	7	63
92	N	meso	9	22	41
93	N	meso	9	11	77
94	N	meso	7	14	70
95	N	meso	6	16	73
96	N	meso	6	16	79
97	N	meso	5	20	83
98	N	meso	5	20	63
99	N	meso	4	25	84
100	N	meso	1	100	100
101	N	meso	8	12	73
102	N	meso	1	100	100
103	N	meso	1	100	100
104	N	meso	19	10	72
105	N	meso	3	33	71
106	N	meso	6	16	82
107	N	meso	3	33	66
108	N	meso	1	100	100
109	N	meso	1	100	100
110	F	meso	3	33	71
111	N	meta	7	14	45
112	N	meta	6	33	60
113	N	meta	1	100	100
114	N	meta	4	25	50
115	N	meta	1	100	100
116	N	meta	2	50	87
117	N	meta	3	33	50
118	N	meta	1	100	100
119	N	meta	11	9	78
120	N	meta	3	33	33
121	N	meta	1	100	100
122	N	meta	7	28	78
123	N	meta	2	50	83
124	N	meta	3	66	95
125	N	meta	3	66	92
126	F	meta	5	20	42
127	N	meta	1	100	100
128	N	meta	7	28	50
129	M	meta	4	50	50
130	F	meta	8	25	86
131	N	meta	3	33	84

Character	Sex	Tagma	length	CI	RI
132	N	meta	1	100	100
133	F	meta	1	100	100
134	F	meta	4	25	62
135	N	meta	3	33	50
136	M	meta	2	50	0
137	M	meta	6	16	61
138	M	meta	1	100	100
139	M	meta	4	50	71
140	M	meta	2	50	0
141	M	meta	4	50	71
142	M	meta	2	50	87
143	M	meta	2	50	50
144	M	meta	3	33	0
145	M	meta	5	40	80
146	M	meta	6	16	79
147	M	meta	1	100	100
148	M	meta	6	16	66
149	M	meta	1	100	100
150	M	meta	4	25	25
151	M	meta	14	21	45
152	M	meta	7	14	57
153	M	meta	6	33	75
154	M	meta	4	50	50
155	M	meta	1	100	100
156	F	meta	3	33	77
157	F	meta	2	50	94
158	F	meta	5	20	80
159	F	meta	10	10	35
160	F	meta	5	60	85
161	F	meta	11	18	67
162	F	meta	1	100	100
163	F	meta	2	50	50
164	F	meta	8	12	73
165	F	meta	12	16	65
166	F	meta	2	50	85
167	F	meta	2	50	50
168	F	meta	3	33	71
169	F	meta	3	66	66
170	F	meta	5	20	42
171	F	meta	7	14	71
172	F	meta	2	50	87
173	F	meta	1	100	100
174	F	meta	1	100	100
175	F	meta	2	50	0

CHAPTER III: Systematics of the parasitoid wasps *Exochus albiceps* species-group (Hymenoptera: Ichneumonidae: Metopiinae)

INTRODUCTION

Exochus Gravenhorst 1829 is the largest genus in the parasitoid wasp subfamily Metopiinae, comprising about 290 species (Choi *et al*. 2016). It is cosmopolitan, with most described species known from the Northern Hemisphere (Yu *et al*. 2012, Gauld & Sithole 2002), and numerous undescribed species in tropical regions (Gauld & Sithole 2002, pers. obs.).

Although *Exochus* is the largest genus and with the widest distribution in the subfamily, little is known about the relationships among its species. Townes & Townes (1959) reviewed the Nearctic species of *Exochus* and characterized twelve species-groups, but these were not adopted by Gauld & Sithole (2002) in their revision of the Costa Rican metopiines, because many species complexes are ill defined, while some species are morphologically distinctive and would form their own species-group. In addition, the monophyly and applicability of these groups has not been previously tested. A species-group suggested by Townes & Townes (1959), the *albiceps* species-group, was recently found to be putatively monophyletic (see Chapter II) and is the focus of the present chapter.

Within the *albiceps* species-group Townes (1972) recognized two species—*E. albiceps* Walsh, 1873 and *E. tegularis* Ashmead, 1894—although he mentioned the occurrence of six undescribed species in the Neotropical region. The *albiceps* species-group was characterized by Townes & Townes (1959) based on having a distinct sternaulus and extending about 0.3× the length of the mesosternum, lacking an occipital carina, and possessing a propodeum with well-defined transverse and longitudinal carinae.

Members of the *albiceps* species-group are among the most commonly collected Ichneumonidae in Costa Rica (Gauld & Sithole 2002) and the Neotropical region (pers. obs.). Besides being an important component of the ichneumonid fauna, their systematics are poorly understood. The aim of this chapter is to test whether the *albiceps* species-group is a natural group and to infer the relationships among its species, based on both molecular and morphological characters. Based on this, the known species within this group are revised and a key provided to the complete diversity of the species group. New data on species distributions, including new country records for both the genus and species, are reported. The information generated in this chapter forms the basis for examining ecological diversity within the species-group (see Chapter IV).

MATERIAL AND METHODS

Depositories of material examined

Specimens from the following repositories (acronyms used throughout the text) were examined for comparative morphological study, molecular extractions (specified in each case throughout the text), and to compile distribution data:

USUC Utah State University, Logan, Utah, USA (David Wahl).

CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (Andrew Bennett).

FSCA Florida State Collection of Arthropods, Gainesville, Florida, USA (Kyle E. Schnepp).

INPA Coleção de Invertebrados do Instituto Nacional de Pesquisas da Amazônia, Amazonas, Brazil (Marcio L. Oliveira).

MEKRB Entomological Museum Klaus Raven Buller, Lima, Peru (Alexander Rodríguez Berrio).

MNCR Museo Nacional de Costa Rica, Santo Domingo de Heredia, Costa Rica (Guisella Chávez Guevara).

MUSM San Marcos Natural History Museum, Lima, Peru (Diana Silva).

NBCN Naturalis Biodiversity Center, Leiden, Netherlands (Frederique Bakker).

SEMC Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA (Michael. S. Engel).

All previously described species of *Exochus* from the Neotropical Region (De Melo *et al*. 2015, Gauld & Sithole 2002) were examined with the aim of determining which species belong to the *albiceps* species-group. The aforementioned species described by Gauld & Sithole (2002) were determined to belong to the species-group.

Photomicrography and Maps

Photomicrographs were prepared using a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscopic lens, stacked in Zerene Stacker, and then arranged in Adobe Photoshop and Illustrator CC2017. Distribution maps were prepared using SimpleMappr (Shorthouse 2010), based on the collection data of specimens and occurrence data recorded in the literature.

Taxon sampling and Outgroups

Fourteen taxa within *Exochus* were selected for phylogenetic analysis. The ingroup included 11 species (including both described and undescribed species) and three outgroup taxa (see Appendix 4). For the molecular analyses several individuals per taxa were included (see Appendix 5). Three species, considered to be part of the ingroup, were only available for morphological analysis. These species were represented by specimens that were too old to easily retrieve quality genetic material (e.g., >50 years old). The individuals used for

molecular extractions are listed in the Appendix 5. The outgroup consisted of three species of *Exochus* (see Appendices 4, 5), which were included in morphological and molecular phylogenetic analyses. The tree was rooted with *Exochus* sp.12 (this species fits with the definition of the *pullatus* species-group *sensu* Townes & Townes 1959).

Morphological Character Selection

Morphological characters were selected based mainly on female individuals, as the males are only known for five species of the *albiceps* species-group. A data matrix (Appendix 6) of 14 terminal taxa, eleven for the ingroup plus three outgroup taxa, and 13 discrete morphological characters from the morphology of the adults, comprising 30 different states (list below) was compiled for this cladistic analysis. A list of characters, as well as definitions of character states are presented below. All characters (either binary or multistate) were coded in Mesquite 2.75 (Maddison & Maddison 2010) and treated as unordered and unweighted. Character states of species for which genitalia or one of the sexes could not be examined (because males are unknown for these species) were scored with '?' and treated as missing data, while a dash (–) was used when a character was not applicable.

A list of morphological characters:

0. Antennomere 2, in lateral view, female: (0) between 1.1–1.2 times; (1) between 1.5–1.9 times.
1. Lower mandibular tooth: (0) directly below upper; (1) turned under (Fig. 27B).
2. Occipital carina: (0) present; (1) absent.
3. Epicnemial carina: (0) complete; (1) interrupted.
4. Epicnemial carina, between sternaulus and subalar: (0) convex, homogeneously; (1) sinuate.

5. Sternaulus: (0) absent, at most extending for at least 0.1× the length of the mesosternum; (1) distinct, extending for at least 0.3× the length of the mesosternum
6. Hind wing with length of abscissa of Cu1 between Cu1 and 1A: (0) 0.1–0.3 times as long as length of vein Cu1 between M and Cu; (1) 0.5–0.9 times as long as length of vein Cu1 between M and Cu.
7. Anterior transverse carina of propodeum, between lateromedian longitudinal carinae: (0) absent; (1) present.
8. Posterior transverse carina of propodeum: (0) complete (Fig. 32B); (1) absent between lateromedian longitudinal carinae (Fig. 35B).
9. Propodeum with lateral longitudinal carina anterior to spiracle: (0) absent (Fig. 39C); (1) present (Fig. 40D).
10. Tergite III, female: (0) unicolorous (Fig. 40A): (1) laterally with a different color (Fig. 30A, Fig. 43B).
11. Malar space, female: (0) less than basal mandibular width; (1) more than basal mandibular width.
12. Paramere, in lateral view, dorsally, preapically: (0) straight; (1) concave; (2) convex.
13. Metasomal tergites VIII+IX of male medially: (0) divided; (1) not divided.

Morphological Phylogenetic Analyses

Searches for the most parsimonious trees (MPTs) were conducted using the heuristic 'New Technology search' algorithm of TNT (version 1.5) using equally weighted settings (Goloboff & Catalano 2016), with 1000 random addition sequences, heuristic searches were performed using multiple tree bisection and reconnection (TBR) branch swapping, holding 100 trees during each replication. Character state changes were mapped onto the tree using Winclada 1.00.08 (Goloboff *et al*. 2003). As more than one most parsimonious tree was

obtained, a strict consensus tree was calculated with Winclada. To evaluate branch support, Bootstrap (BS) and Jacknife (JS) support values were calculated using TNT (Goloboff *et al*. 2003), the values were mapped onto (BS) and below (JS) the internal nodes of the tree.

Molecular Phylogenetic Analyses: Laboratory Methods

Genomic DNA was extracted from the sample tissue using standard protocols for the Dneasy Blood and Tissue Kit (Qiagen, Düsseldorf, Germany). The sampled specimens had been variously preserved in either 95% ethanol, 70–80% ethanol, or dried. In most cases, one or two legs were ground for tissue lysis, but for some taxa the entire body was soaked and retrieved after lysis.

Three gene regions were amplified: mitochondrial *NADH dehydrogenase 1* (ND1), and nuclear *28S rRNA* (28S) and *wingless* (Wg). Amplifications were conducted using published primers (Appendix 7). Different loci had various degrees of success in amplification and sequencing (see Appendix 5).

Amplifications were performed in 25 μL using 2.0 μL of template DNA, 1.0 μL of each primer at 10 μm concentration, and 12.5 μL of GoTaq® Hot Start Green Master Mix (Promega Corporation (Madison, WI, United States) with various thermocycler programs (Appendix 6). Amplified samples were purified with Agencourt AMPure XP beads (Beckman Coulter, Brea, CA, U.S.A.). Sequencing was performed in both directions in a 96-well ABI PrismTM 3730xl automated DNA sequencer (Applied Biosystems, Inc., Foster City, CA, U.S.A.).

The resulting sequences sequence, alignment length is 1558 bp, reads of respective genetic markers were assembled, cleaned, trimmed aligned (via MAFFT; Katoh & Standley 2013) and concatenated using Geneious v. 10 (http://www.geneious.com, Kearse *et al*. 2012).

Molecular Phylogenetic Analyses: Computational Methods

Maximum Likelihood (ML) analyses of molecular data were run using W-IQ-TREE (Trifinopoulos *et al*. 2016), with the online web application version of IQ-Tree (Nguyen *et al.* 2015). Gene trees were constructed using default settings, with substitution models selected using the embedded search function (substitution model: "Auto") and 1,000 ultrafast bootstrap replicates (Minh *et al.* 2013, Hoang *et al*. 2018). Respective alignments of each marker were not partitioned for construction of individual gene trees. ML analysis of the concatenated molecular dataset were conducted as above, however each the dataset was partitioned a priori by respective markers, with protein coding genes (ND1, Wg) partitioned by codon. Maximum Likelihood analyses of the total-evidence dataset were run using IQ-TREE v. 1.6.2 (Nguyen *et al*. 2015). The dataset was partitioned *a priori* as in other analyses, with the morphological matrix treated as a single data subset and the molecular matrix partitioned by gene and codon as above. Substitution models for each data subset were selected using the IQ-TREE default model search algorithm ModelFinder (Kalyaanamoorthy *et al*. 2017; "-m MFP" command, but including the "+MERGE" option which also tests the merged partitions to find the optimal partitioning scheme). This was done via the edge-linked partition model (Chernomor 2016; "-spp" option), in which all partitioned subsets share the same underlying branch lengths but are allowed their own independent evolutionary rates. Nodal support of the ML tree was assessed by 1,000 ultrafast bootstrap replicates (Minh *et al*. 2013; Hoang *et al*. 2018; "-bb 1000" command). An ultrafast bootstrap value (UFB) of 95 is considered the threshold for high support of a given node (Minh *et al*. 2013, Hoang *et al*. 2018).

RESULTS

The different analyses including various sets of data types yielded conflicting results. The *E. albiceps* species-group was well supported by morphological characters and poorly supported by the gene 28S and the combined molecular and morphological analysis. The genes ND1 and Wg had low coverage (see below) and could not provide evidence for the status of the species-group as well as the relationships among the species. Therefore, morphology is currently the only basis for the circumscription of the *albiceps* species-group.

Three species are newly assigned to the species-group: *E. ablatus* Gauld & Sithole, 2002, *E. izbus* Gauld & Sithole, 2002, and *E. jacintus* Gauld & Sithole, 2002. Another six new species from the Neotropical region are also found in this species-group; provisionally, they are denoted as: *Exochus* 1 sp. nov., *Exochus* 2 sp. nov., *Exochus* 4 sp. nov., *Exochus* 5 sp. nov., *Exochus* 7 sp. nov., and *Exochus* 8 sp. nov. The complete diagnosis and description of the species group is provided in the taxonomic part below.

Morphological Phylogenetic Analysis

The *E. albiceps* species-group was well-supported by morphological characters. The parsimony analysis resulted in three MPTs (TL = 26, CI = 57, RI = 63), with four collapsed nodes in the consensus tree (Fig. 21). The shape of the mandible, with the lower tooth turned under the upper tooth (1-1), was found as a synapomorphy for the species-group. The presence of the anterior transverse carina of propodeum between the lateromedian longitudinal carinae (7-1) is also unique within the species-group in comparison with the outgroup, but this feature can be found in other *Exochus* species (Gauld & Sithole 2002, Townes & Townes 1959) that were not included in this study. The medially divided metasomal tergites VIII+IX of male (13-0), is uniquely found in this species-group but only

five species could be examined for this feature. I expect that this is potentially a synapomorphy for this species group.

One of the most distinctive features of the *albiceps* species-group is the area superomedia and dentipara enclosed, because the carina posterior transverse is complete (8-0, Fig. 30D). This character-state is reversed in *Exochus* 1 sp. nov. (8-1, Fig. 35B), in which several carinae of the propodeum seem to have been lost secondarily.

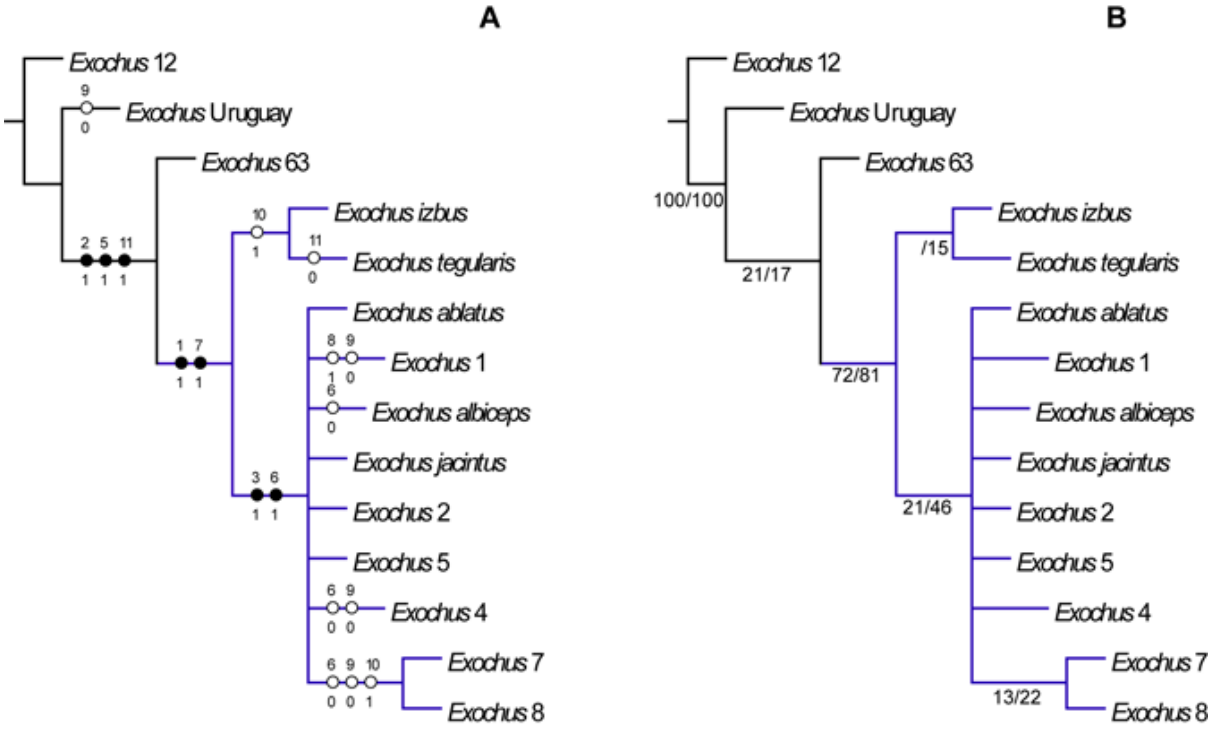

Figure 21. The strict consensus tree of three equally most-parsimonious trees, inferred from morphological data. **A.** Tree with all character state changes mapped upon it. **B.** Tree with branch support values are displayed below the nodes in the following order: Bootstrap and Symmetric sampling values. When no value is shown it refers as values could not be estimated. Ingroup in blue.

The relationships among the species of the albiceps species-group could not be resolved in the phylogeny inferred from morphological data; except for the well-supported sister relationship of *E. izbus* and *E. tegularis*, and this clade being sister to the remaining members of the group. Additionally, *Exochus* 7 sp. nov. (Fig. 42) and *Exochus* 8 sp. nov. (Fig. 43) are sister; these two species present similar coloration (see Taxonomy section) and an almost identical morphology.

Exochus albiceps (Fig. 28) and *Exochus* 4 sp. nov. (Figs. 38, 39) exhibit strong sexual dimorphism regarding overall coloration. For this reason, character ten was restricted to the female sex. For those species where males are unknown, the male could have a different coloration relative to corresponding their females. For this reason, a rather conservative approach was taken and only females were code for this character. Including additional characters based on coloration (such as the color of the metatibia) which are strongly related with sex could have generated more uncertainty to the analyses.

Molecular Phylogenetic Analysis

The individuals used for the molecular extraction are shown in Appendix 5, as well as the data capture method for each one; 37 individuals were included in this part of the study, for all of them were obtained sequences for the marker 28S, while for the gene regions ND1 only for eight individuals and for the gene Wg only for seven individuals. Most of the sequences obtained for ND1 and Wg were found in the outgroups, leaving few for the ingroup (Appendix 5).

The nuclear ribosomal **28S** gene (Fig. 22) was only the gene had good coverage and that resulted in well-resolved tree. With this marker, the *albiceps* species-group was recovered as monophyletic but with low support (BS=63). Due to the conserved nature of the 28S gene, species delimitations were unclear (see Appendix 8). Three subgroups were recovered but with low support; these subgroups show some congruence with a pattern found in the morphological revision. The subgroup that includes the species *E. jacintus* (Fig. 32), *Exochus* 1 sp. nov. (Fig. 35), and *Exochus* 5 sp. nov. (Fig. 40) are characterized by having a brown metatibia; the subgroup that includes *E. izbus* (Fig. 30) and *E. tegularis* (Fig. 34) has an off-white and dorsally brown metatibia; and the subgroup that includes *Exochus* 4 sp. nov.

(Fig. 39), *Exochus* 7 sp. nov. (Fig. 42), and *Exochus* 8 sp. nov. (Fig. 43) has an entirely tawny metatibia.

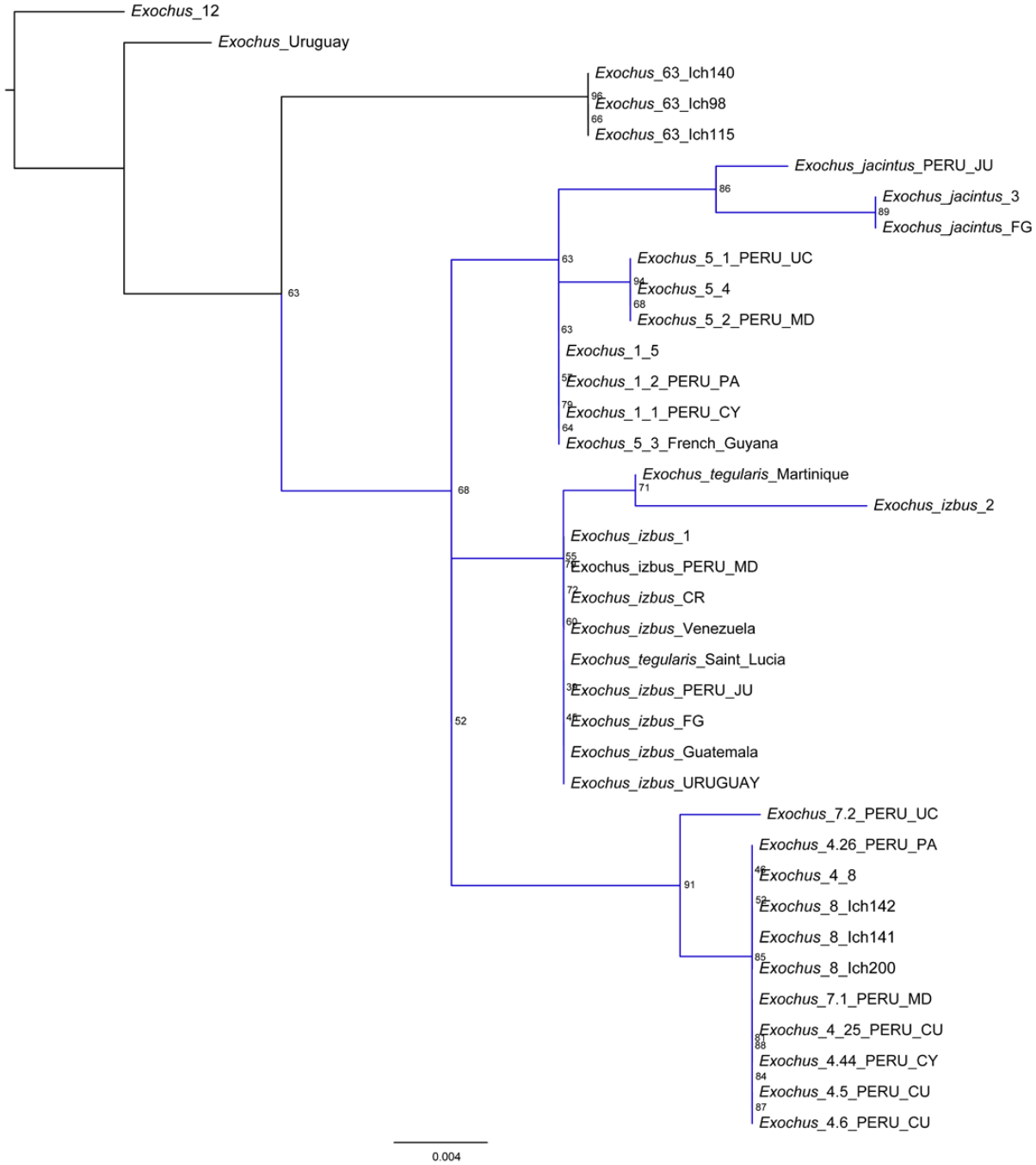

Figure 22. Tree resulting from analysis of gene 28S. Maximum Likelihood analysis with 1,000 replicates. Values at nodes indicate ultrafast bootstrap support. Ingroup in blue.

The genes **ND1** (Fig. 23) and **Wg** (Fig. 24) did not recover the *albiceps* species-group as monophyletic, nor any relationships among the species due the lack of coverage. Despite the fact that Wg was sequenced only for seven individuals (Fig. 24), three of them were

considered a prior to belong to *Exochus* 8 sp. nov. The individual *Exochus*_8_Ich200 has lower values in the matrix of genetic distances than the individuals *Exochus*_8_Ich141 and *Exochus*_8_Ich142 (see Appendix 10). These lower values in comparison to the other two individuals indicates greater genetic distance between the individuals; this difference could be considered enough to be a distinct species. ND1 was not sequenced for *Exochus*_8_Ich200, and the three individuals have identical sequences within 28S. These individuals were collected close to each other, but at different elevations, *Exochus*_8_Ich141 and Exochus_8_Ich142 were collected at 1593m while *Exochus*_8_Ich200 was collected at 1940m. Until more molecular evidence is recorded for these two populations, they are considered as members of the same species, from a strictly morphological perspective they would belong to a single species but the potential for cryptic species cannot be ruled out.

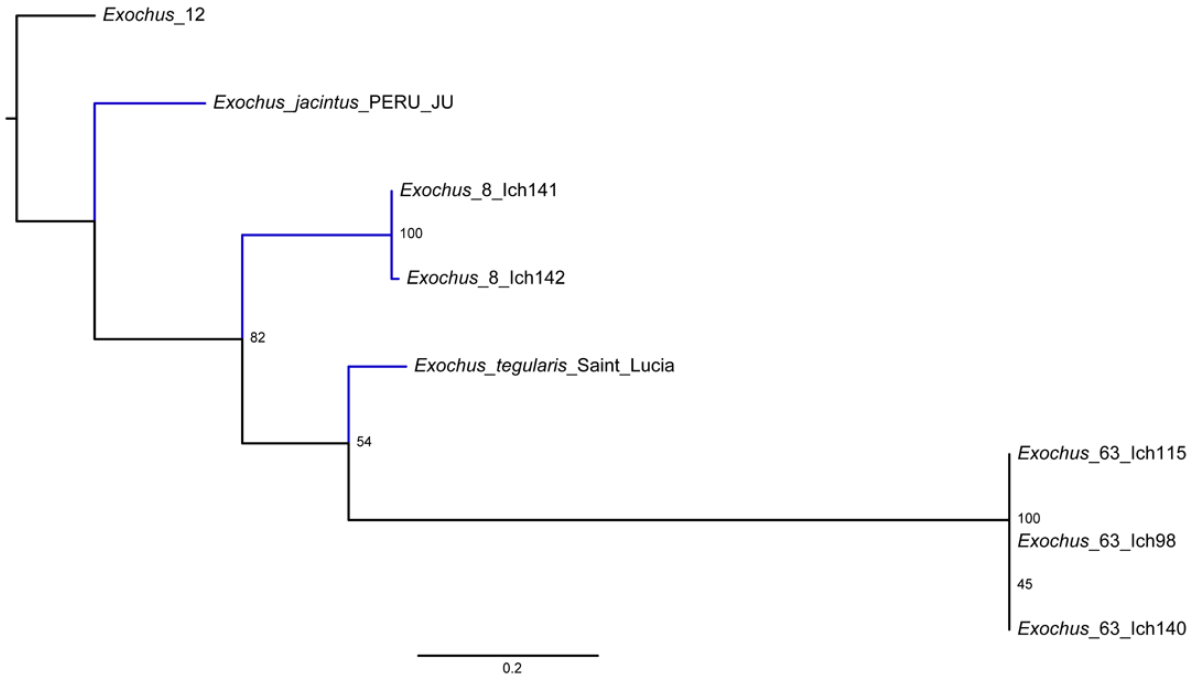

Figure 23. Tree resulting from analysis of gene ND1. Maximum Likelihood analysis with 1,000 replicates. Values at nodes indicate ultrafast bootstrap support. Ingroup in blue.

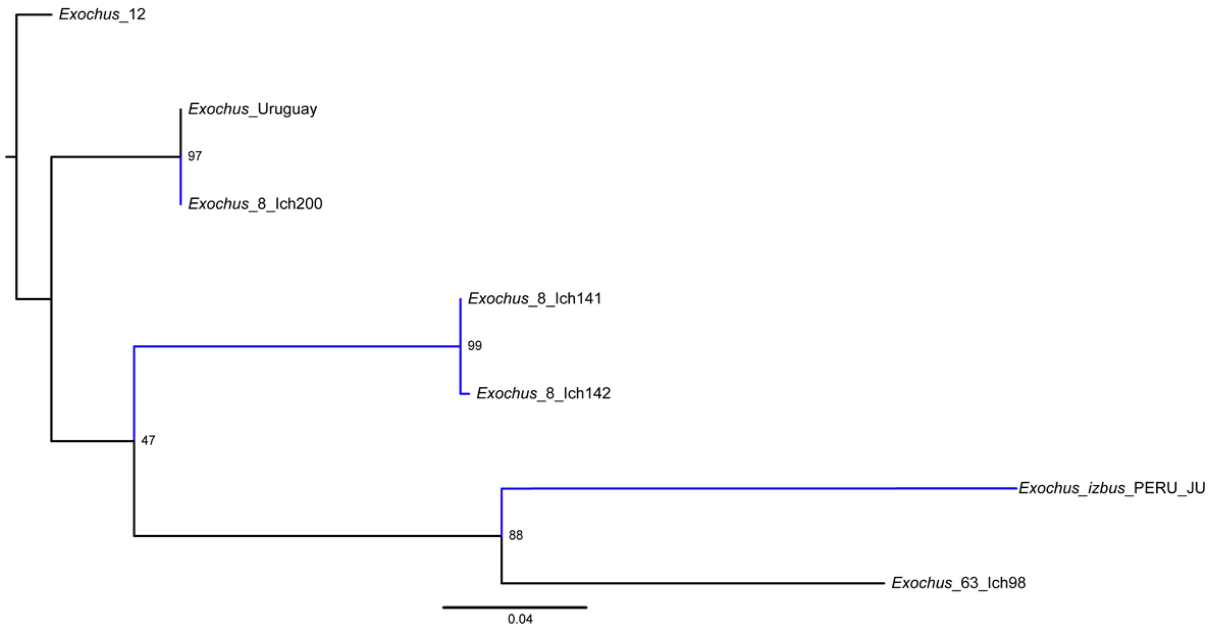

Figure 24. Tree resulting from analysis of gene Wg. Maximum Likelihood analysis with 1,000 replicates. Values at nodes indicate ultrafast bootstrap support. Ingroup in blue.

The resulting tree from the **combined analysis of molecular data** (Fig. 25) did not recover the *albiceps* species-group as monophyletic. The outgroup *Exochus* 63 fell within the ingroup (Fig. 23); the influence of the low coverage for the genes ND1 and Wg was reflected in this result.

The resulting tree from the **combined analysis of molecular and morphological data** (Fig. 26) has slightly better support than the tree obtained for 28S. This analysis found the *albiceps* species-group as monophyletic with good support (BS=89). The only clade with high support within the species-group is the cluster including the individuals of *E. izbus* and *E. tegularis* (BS=98). This clade was also recovered by 28S and the morphological analysis, but with lower support.

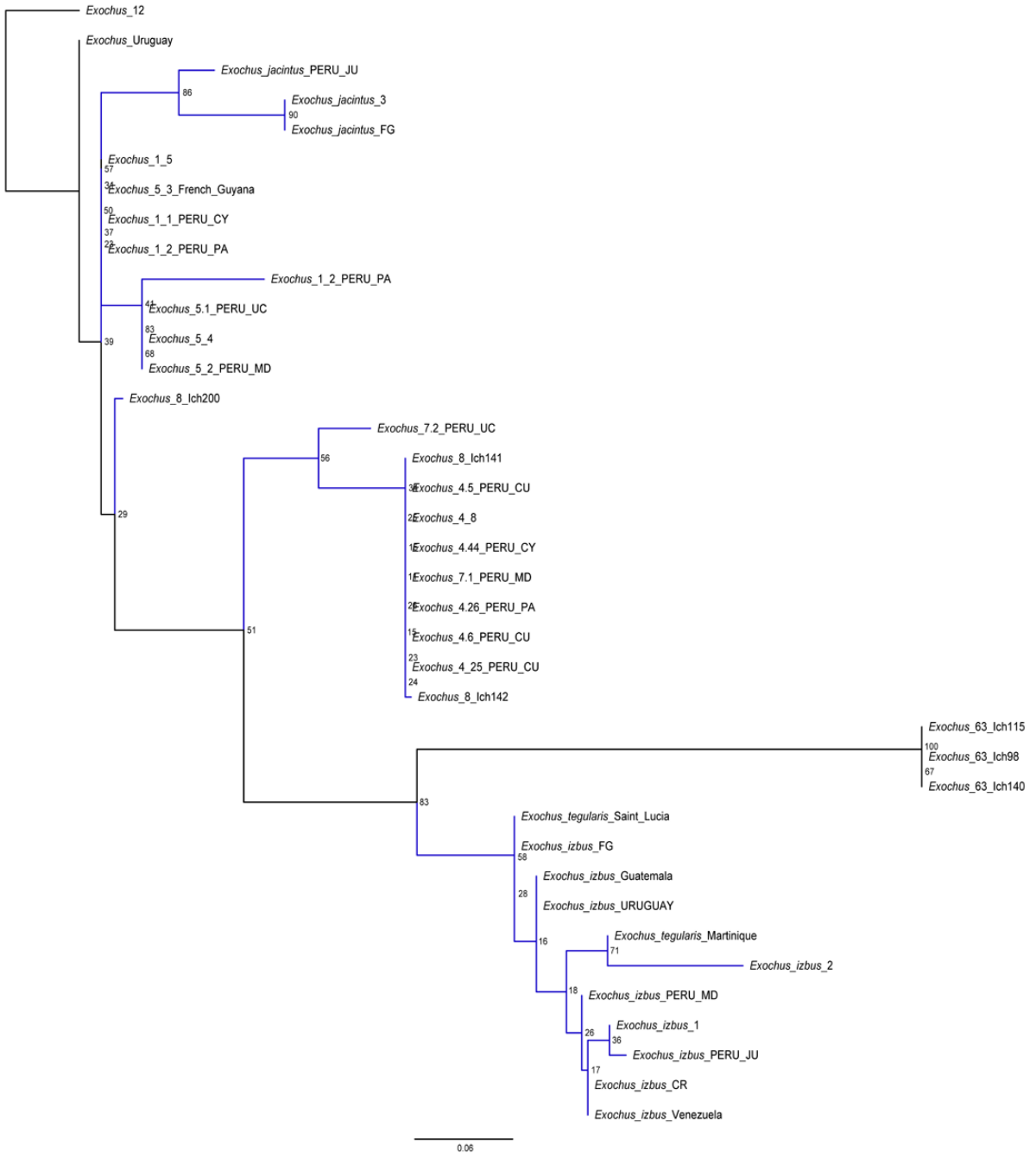

Figure 25. Tree resulting from combine molecular data (including 28S, ND1, and Wg). Maximum Likelihood analysis with 1,000 replicates. Values at nodes indicate ultrafast bootstrap support. Ingroup in blue.

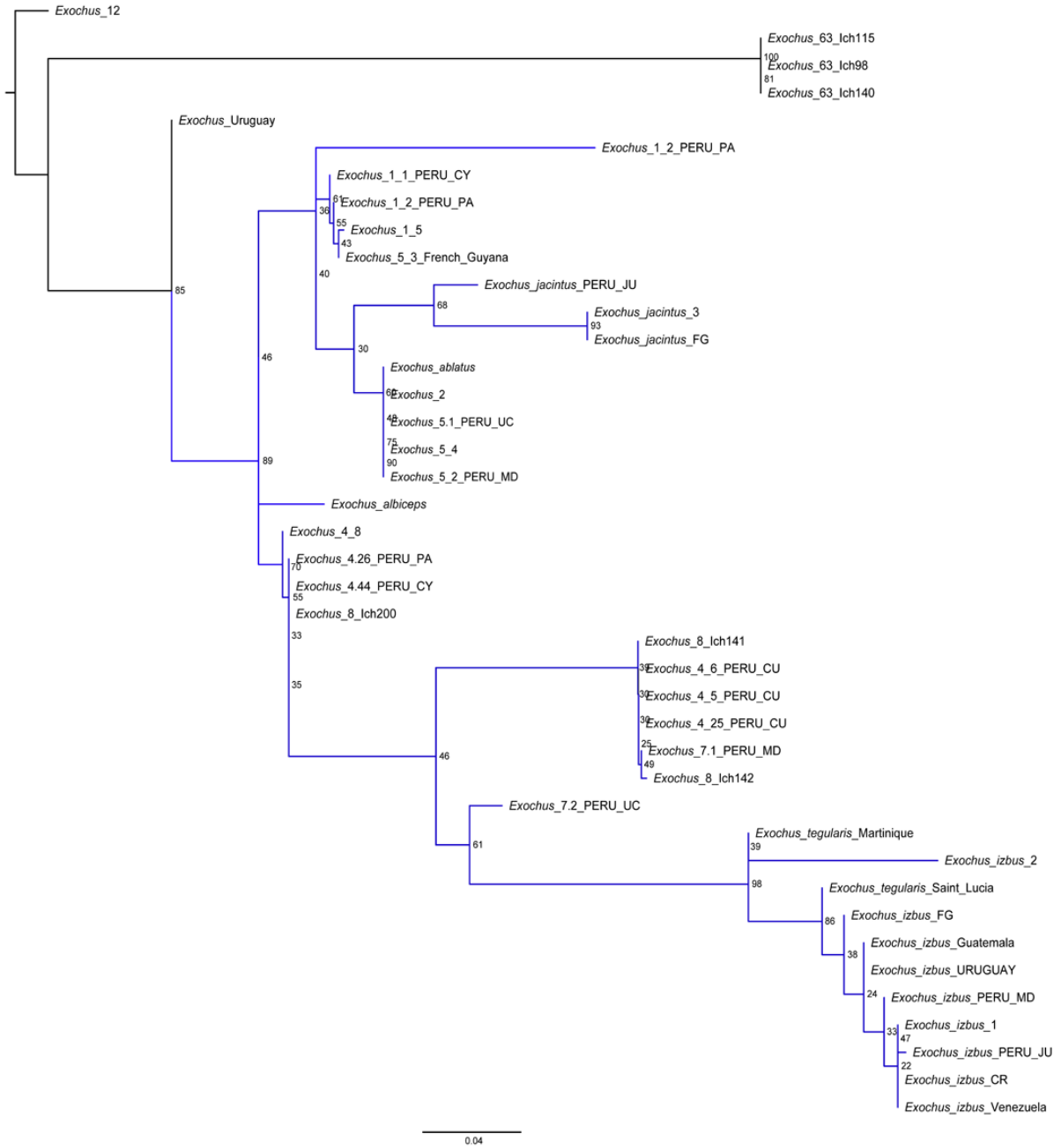

Figure 26. Tree resulting from combine molecular and morphological data. Maximum Likelihood analysis with 1,000 replicates. Values at nodes indicate ultrafast bootstrap support. Ingroup in blue.

Despite the low support for the tree, the subgroup that includes the species *E. jacintus*, *Exochus* 1 sp. nov., and *Exochus* 5 sp. nov., was also recovered in this analysis but including the species *E. ablatus* and *Exochus* 2 sp. nov., for which molecular data was missing. All these species have a brown metatibia, also have the hind wing with the length of abscissa of Cu1 between Cu1 and 1A 0.5–0.9 times as long as the length of vein Cu1 between M and Cu (6-1). *Exochus albiceps* (Fig. 28), in both sexes, has the metatibia off-white and dorsally

brown, like the subgroup that includes *E. izbus* (Fig. 30) and *E. tegularis* (Fig. 34); but they do not cluster together.

Species discovery and delimitation

Six species are described, and two re-described (see taxonomic part below). The three Costa Rican species were recently described (Gauld & Sithole 2002) so were not re-described, but a diagnosis is presented for each one to incorporate the new features and to compare them with the new species described here. The species circumscription was based on their morphology, as the molecular analyses lacked coverage and did not allow for the delimitation of the taxa. Useful characters to circumscribe the species are: the length of the abscissa of Cu1 between Cu1 and 1A in the hind wing (character 8), dimensions of the metasomal tergites, number of antennomeres (e.g., Figs. 27A, 34A), and the coloration of legs (e.g., Figs. 27A, 28A) and metasomal tergites (e.g., Figs. 27A, 30A, 43B).

Due to the strong sex bias, several species are known only from females. This was found for species widely distributed and quite commonly collected like *E. jacintus*, as well as for species rarely collected, such as *Exochus* 2 sp. nov. and *Exochus* 8 sp. nov. For this reason, the description of the species is based on females, but differences in the males are mentioned where known.

Of the eleven species, *E. izbus*, *E. jacintus*, *Exochus* 5 sp. nov., and *Exochus* 7 sp. nov. occur in lowland wet sites (elevation range is presented in the taxonomic part), *E. ablatus*, *Exochus* 1 sp. nov., *Exochus* 4 sp. nov., and *Exochus* 8 sp. nov. occur at mid to high elevations on the slopes of mountainous regions, *E. albiceps* is the only Nearctic species, and *E. tegularis* is only found in the Caribbean islands.

DISCUSSION

Exochus is the largest genus of the subfamily Metopiinae and the major relationships among the species are far from understood (Gauld & Sithole 2002). The intention of this study was to test the monophyly of the *albiceps* species-group and to infer the internal relationships. This species-group was defined to include the Nearctic species *E. albiceps* (Townes & Townes 1959); and it was subsequently noticed that the richness of this group is centred in the Neotropical region (Townes & Townes 1959, Townes 1972). The features used by Townes & Townes (1959) to characterize the *albiceps* species-group are not synapomorphies for this group. There is only one unambiguous synapomorphy for this group, the shape of the mandibles (1-1) which are apically twisted, so that the lower tooth is turned under the upper. This feature was probably not considered as characteristic of this species-group because when the group was described the study concentrated on the Nearctic species.

The morphological phylogeny supports the monophyly of the species-group but fails to resolve relationships among the species. Few characters were employed for the morphological dataset as the species are morphologically quite similar, and there are few features that allow for their separation (see taxonomy part). Among the most reliable features are patterns of coloration, but this must be considered carefully. After analyzing several individuals per species, the color of the metasomal tergites was found to be reliable and was used in this study. Another informative character is the length of the abscissa of Cu1 between Cu1 and 1A in the hind wing (character 8), and the presence or absence of the lateral longitudinal carina anterior to the propodeal spiracle (character 9).

Many features were not coded owing to the rarity of the species involved, so only a single sex could be examined, and dissections were not possible. Thus, many critical and informative features are missing for these species in the present analysis. Features of male genitalia could be informative, the parameres exhibit different shapes (see character list) but

several species are only known from females. Once more males are found, it may be possible to test if some sex-linked features, like the different coloration between the sexes of *E. albiceps* and *Exochus* 4 sp. nov., have a phylogenetic signal or not. The rarity of the species may be related to the distribution of the species, as some of them are distributed at mid to high elevation locations that are rarely sampled owing to difficult access. Additionally, the strong sex bias within several species collected may be linked to the fact that the females are constantly looking for potential hosts, making them more susceptible to entrapment relative to males.

Exochus 8 sp. nov. can be found on the slopes of the Andes between 1600–2170m. The gene Wg found two distinctive populations (or at least genetic distance); these populations are separated by ~340m of elevation. It is worth revisiting this species, including more molecular markers, with the aim of determining whether these individuals constitute a single taxon or multiple cryptic species. One limitation is that they are known only from four individuals, and they are restricted to a wet forest of Chanchamayo in Peru. Further, two species encountered on the slope of the Andes, *Exochus* 1 sp. nov. and *Exochus* 4 sp. nov. (see taxonomy part), which were only sequenced for 28S, should also be revisited with less conserved genetic data from a phylogeographic perspective, and to explore the influence of elevation on populations.

In this study, only 28S was effectively sequenced for most of the species. The molecular data for the other two markers was poorly captured. The molecular section of the study needs to be revisited, and taking into account other approaches. The first approach that should be taken is the consideration of adding different markers, such as mitochondrial cytochrome oxidase I (COI) and 16S rRNA (16S). These two markers have been employed previously in analyses of ichneumonids (Veijalainen *et al*. 2011, Santos 2017, Klopfstein *et al*. 2011), and yielded promising results. Another approach could be designing new primers

to improve amplification in more difficult specimens; and lastly, considering the use of phylogenomics, such as ultraconserved elements which work with suboptimally preserved specimens and/or degraded DNA and have been successfully employed in Hymenoptera (Branstetter *et al*. 2017, Faircloth *et al*. 2015).

Further work is needed both in deepening the taxonomic sampling and in augmenting the character sets by the addition of more molecular data. This will help to provide a more complete picture of the phylogeny of the *albiceps* species-group, contributing towards better taxonomic work and underpinning the investigation of the evolutionary processes that generated diversity within the group.

TAXONOMIC PART

Terminology

Morphological terminology and the format for descriptions generally follow that of Gauld & Sithole (2002). The biometric ratio of the face+clypeus was measured at the narrowest point for width and from the lower level of the pre-antennal flange to the median clypeal margin for length. The length of flagellomeres was measured in lateral view, and their individual widths were measured at their widest points. Only diagnoses were provided for *E. ablatus*, *E. izbus*, and *E. jacintus* as these species were recently described in detail (Gauld & Sithole 2002).

Taxonomic History

Townes & Townes (1959) reviewed the Nearctic Metopiinae and as part of that work 12 species-groups were proposed for the genus *Exochus*. One of the species-groups was based on *Exochus sulcatus* Townes & Townes, 1959, which was described from a single male individual. A female specimen from Venezuela was suggested to be conspecific or of a

closely related species (this is clarified below) by Townes & Townes (1959), but in Yu *et al*.'s (2012) catalog this species was considered as conspecific with *E. sulcatus*.

Subsequently, Townes (1972) synonymized *E. sulcatus* with *E. albiceps* Walsh, 1873, as he examined a series that included males and females. The type series of *E. albiceps* was destroyed by fire in Chicago in 1971 (Townes 1972). Walsh (1873) described *E. sulcatus* from a male individual, but Townes (1972) noticed that the female individuals agreed with the description done by Walsh (1873) and assumed that Walsh had misidentified the sex, as this species exhibits sexual dimorphism in overall coloration. Based on this synonymy, the species-group was renamed based on *E. albiceps*; additionally, Townes (1972) included *E. tegularis* Ashmead, 1894, and recognized six undescribed species from the Neotropical region to be members of this species-group.

The 51 described Neotropical species of the genus were reviewed (De Melo *et al*. 2015, Gauld & Sithole 2002), and *E. ablatus* Gauld & Sithole, 2002, *E. izbus* Gauld & Sithole, 2002, and *E. jacintus* Gauld & Sithole, 2002, agree with the definition of the *albiceps* species-group.

Systematics

Exochus albiceps species-group

Diagnosis. Mandibles, strongly tapered to a fine point (mandible apically less than 0.3× as broad as base), apically twisted, so that when mandibles are closed they appear more or less unidentate and needle-sharp; occipital carina absent; epicnemial carina complete, generally preapically evanescent; sternaulus distinct and extending about 0.3× length of mesosternum; propodeum generally with anterior and posterior transverse carinae well defined as well as longitudinal carinae, so area superomedia and dentipara generally enclosed; metapleuron bare; male with metasomal tergites VIII+IX not divided.

Redescription. *Head.* Mandibles tapering towards apex, 0.2–0.3× as broad as base; bidentate, twisted with lower tooth directly below upper, upper tooth longer than lower tooth; without ventral flange; abductor swelling next to upper corner; mandible without ventral flange; condylar ridge straight, not interrupted, neither turned upwards; next to condylar ridge flat. Labrum not exposed when mandibles closed. Palpal formula 5:4; maxillary palpomeres slender. Clypeus transverse, apical margin straight; without preapical transverse ridge parallel to margin; with sulcus upwards from base of mandible. Face+clypeus moderately convex (tentorial pit not located in elevation); malar space with similar texture as clypeus with distinct groove along whole length; upper part of face produced upwards between bases of antennae, dorsally produced into lamella reaching to toruli; frons without carina surrounding toruli; integument next to toruli without striations; occipital carina absent; postgenal bridge not projected.

Mesosoma. Pronotum polished with band of setae along upper margin, with longitudinal concavity parallel to anterior margin; upper edge without shallow submarginal groove; with pocket-like structure in lower corner, smooth without striae; epomia close to and parallel with anterior margin of pronotum. Propleurae not swollen. Mesoscutum rather flat, with notauli impressed anteriorly; without concavity next to lateral margin, between notauli and tegula; scutoscutellar groove broad, smooth; mesoscutellum tapering towards distal end, with lateral carinae only reaching over prescutellar ridge. Mesopleuron moderately swollen; epicnemial carina complete, laterally convergent with anterior margin of pleuron until near upper end where it turns backwards to reach subalar prominence, generally preapically evanescent; subalar prominence flattened (not forming carina-like projection or horn); sternaulus distinct, extending about 0.3–0.5× length of mesosternum; posterior transverse carina presents laterally and centrally (absent in front of coxae). Metapleuron weakly convex, polished, bare; ventrally with weak submetapleural carina which expand into lobe on anterior half.

Propodeum with lateral longitudinal carinae complete and strong, sometimes evanescent basally; lateromedian longitudinal carinae generally present between base of propodeum and posterior transverse carina (distally absent in *E. acarinatus*); anterior transverse carina present (rarely faint between lateral and lateromedian longitudinal carinae); posterior transverse carina complete, absent medially in *E. acarinatus*; propodeal spiracle elongate. Pro- and mesotrochantellus not differentiated; tibiae distally without dentiform process; protibial spur antero-dorsally with comb and postero-dorsally with velum; protarsomeres 2–3 slightly longer than wide, protarsomere 4 generally wider than long; pretarsal claws simple. Mesotibia with two spurs, outer spur shorter than inner spur. Metatibia with inner margin apically with comb, curved; metatibia with two spurs, outer spur shorter than inner spur; metatarsomere 5 without hooked lobe on inner side of distal metatarsomeres of female. Forewing without enclosed areolet; cu-a far distal to base of Rs&M; 2m-cu with one bulla. Hind wing with distal abscissa of Cu1 joining cu-a closer to 1A than to M.

Metasoma. Tergite I with lateral and lateromedian longitudinal carinae well developed, spiracle 0.3–0.4× of way along tergum; sternum I short, ending anterior to spiracle; laterotergite II 0.1–0.5× as wide as long; laterotergite III 0.4–0.6× as wide as long; laterotergites of metasomal segments III and IV separated by crease; metasomal tergite VI–VIII without setae on distal margin; metasomal tergite VIII of female entirely flat; female with sterna IV–VI weakly sclerotized with membranous area; female with sternum VI wider than long, basally and distally more or less straight. Male with metasomal tergites VIII+IX not divided; sternum VIII wider than long with lateral margins parallel to each other or converging distally; paramere distally forming hood, dorsoventrally flattened; apodemes of aedeagus shorter than aedeagus.

Remarks. This species-group is predominantly Neotropical with a single species inhabiting North America, *E. albiceps.* Most of the species can be found in wet tropical forests from sea

level up to 2,875 m. The species seem to be restricted by ranges of elevation, data for each species is mentioned in each case. With reference to the Andean countries of Peru, Bolivia, and Argentina, they can only be found on the eastern slopes of the Andes (the western slopes of the Andes in these areas are dry). In Ecuador species can be found on both slopes of the Andes as wet forest occurs on both sides. It is likely that the members of the *albiceps* species-group occur in Colombia but as of yet no material has been recorded from this country.

***Exochus ablatus* Gauld & Sithole 2002**

Exochus ablatus Gauld & Sithole, 2002: 82

Figures 27, 29

Diagnosis. Face+clypeus 0.7–0.8× as long as wide; malar space 1.1× as long as basal mandibular width; antenna with 36–38 flagellomeres; mesopleuron with epicnemial carina preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.9× as long as length of vein Cu1 between M and Cu1; propodeum tawny; metacoxa tawny; metatibia predominantly brown; metasoma black with brown laterally at apex of tergites.

Distribution. The species was previously known only from Brazil (De Melo *et al*. 2015) and Costa Rica (Gauld & Sithole 2002); it is recorded here from Panama (Fig. 29). The occurrence record form Brazil does not agree with the description of the species based on the pictures presented by De Melo *et al*. (2015), and this material should be checked in order to confirm the presence of the species in Brazil. This species occurs in wet forests of Costa Rica (Gauld & Sithole 2002) and Panama, between 1,000–1,200 m.

Examined material. Non-type material: ♀ "PANAMA: Chiriqui, L Fortuna Dam, 1200m June 4-July 16 1982; B. Gill" (USUC).

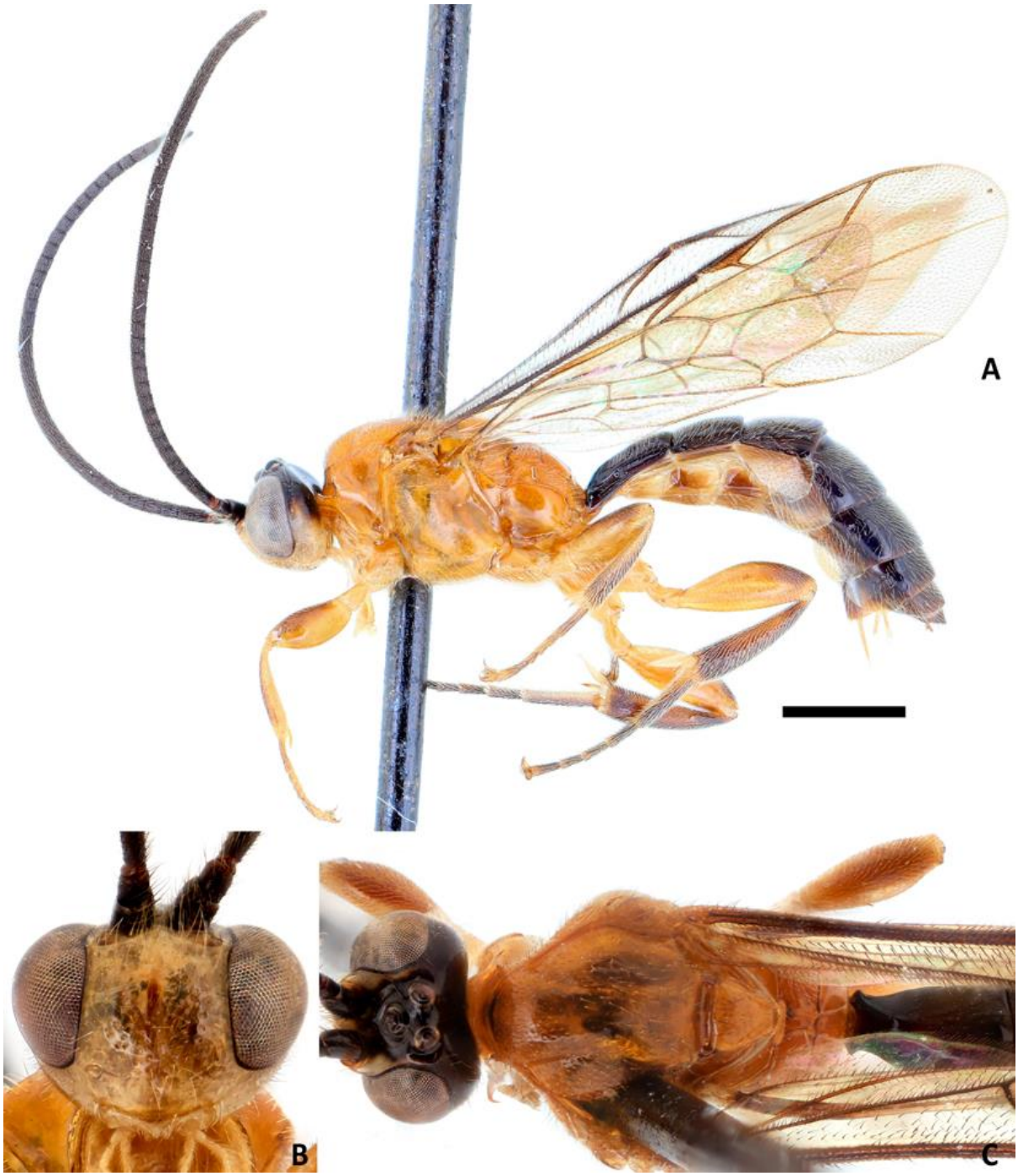

Figure 27. Morphology of *Exochus ablatus* Gauld & Sithole, female (non-type). **A.** Lateral habitus (scale bar=1mm). **B.** Head, facial view. **C.** Dorsal view of head, mesoscutum, and propodeum.

***Exochus albiceps* Walsh 1873**

Exochus albiceps Walsh, 1873: 96. Type lost.

Exochus sulcatus Townes & Townes, 1959: 211. Type lost. Townes 1972: 259 (synonymized with *albiceps*)

Figures 28, 29

Diagnosis. Face+clypeus 0.9× as long as wide; malar space 1.2× as long as basal mandibular width; antenna with 35 flagellomeres; mesopleuron with epicnemial carina preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.2× as long as length of vein Cu1 between M and Cu1; metatibia predominantly off white and dorsally brownish; female with metacoxa off white with tawny longitudinal mark latero-externally, and propodeum entirely tawny; male with metacoxa off white with a blackish longitudinal mark latero-externally, propodeum centrally black, and metasoma black with lateral and distal margins of tergites III–VII off yellow.

Redescription. Female: Forewing length 4.3 mm.

Head. Face+clypeus (Fig. 28B) 0.9× as long as wide; malar space 1.2× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.7× maximum ocellar diameter; distance between ocelli 0.8× maximum ocellar diameter (Fig. 28C); gena in lateral view 0.5× as long as compound eyes; antenna with 35 flagellomeres, ratio of length from second to fourth flagellomeres: 1.0:0.9:0.9, subapical flagellomere elongate, 1.1× as long as centrally broad.

Mesosoma. Mesopleuron with epicnemial carina ending at subalar prominence, preapically interrupted (Fig. 28C). Submetapleural carina smooth, anteriorly expanded into triangular lobe. Propodeum with anterior and posterior transverse carinae complete; lateromedian longitudinal present between base of propodeum and posterior transverse carina; lateral longitudinal carina present; area superomedia 1.3× as long as wide. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.6× its own length; Cu1 between 1m-cu and Cu1a 2.9×

as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.7× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.7× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of M weakly sclerotized; length of abscissa of Cu1 between Cu1 and 1A 0.2× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.7× as long as inner spur.

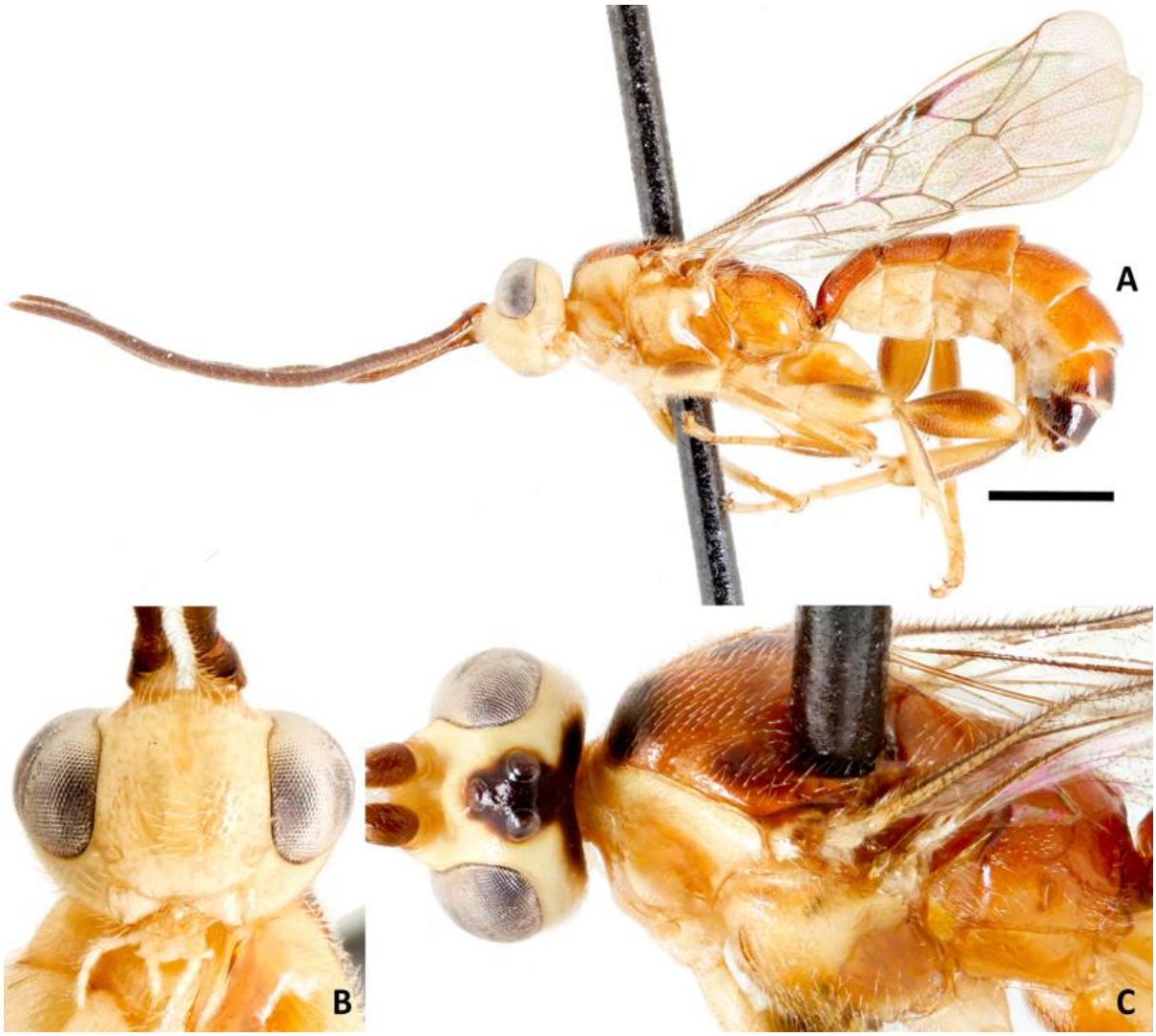

Figure 28. Morphology of *Exochus albiceps* Walsh, female (non-type). **A.** Lateral habitus (scale bar=1mm). **B.** Head, facial view. **C.** Dorsal view of head, mesoscutum, and propodeum.

Metasoma. Tergite I 1.1× as long as posteriorly wide, lateromedian carinae extending 0.6× length of tergite; tergite II 0.6× as long as posteriorly wide; laterotergite II 0.2× as long as wide; laterotergite III 0.6× as long as wide, semicircular, mesal edge convex (Fig. 28A).

Color. Head mostly off white (Fig. 28B) with interocellar area and central part of occiput black (Fig. 28C); antenna brownish black. Mesosoma tawny (Fig. 28A), tegula with distal half brown, gradually changing in upper third off white; mesoscutum anteriorly between notauli, blackish, and anteriorly between lateral margin and notaulus brownish; pro- and mesolegs off white, femurs and tibiae dorsally brownish but off white at joints; metaleg off white, coxa lateroexternally with tawny longitudinal mark, femur laterodorsally and tibia dorsally brown. Metasoma tawny with distal half of tergite VI and VII–VIII brownish.

Male. Similar to female but antennomeres longer, ratio of length from second to fourth flagellomeres: 1.4:1.3:1.3, subapical flagellomere elongate, 1.1x as long as centrally broad. There is variation in the coloration, head mostly off white with interocellar area and central part of occiput black; antennae blackish. Mesosoma off white; mesoscutum brown except notauli area and postero-centrally brownish tawny; tegula, metanotum, postscutellum and propodeum centrally black; legs off white, but femur ventrally, tibia dorsally, and tarsomeres dorsally brownish, metacoxa lateroexternally with blackish longitudinal mark. Metasoma black with lateral and distal margins of tergites III–VII off yellow.

Distribution. *Exochus albiceps* (Fig. 29) is the only species occurring in North America (Townes, 1972), and can be found in Eastern deciduous forest.

Remarks. The material examined by Townes and deposited in USUC was examined. When he described *E. sulcatus* Townes & Townes, 1959, only a male individual was examined, the male could be confused with *E. izbus*, as they have similar coloration. Moreover, the drawings presented by Townes & Townes (1959) were based on a female specimen from Venezuela, which was suggested to be of the same species (Townes & Townes 1959).

Subsequently, Townes (1972) synonymized it with *E. albiceps* as he examined a series that included male and female individuals. He noticed that the male individuals agreed with the description done by Walsh (1873) and assumed that the sex was misidentified as the females have a different coloration. *Exochus albiceps* does not occur in Venezuela, the specimen studied by Townes from this country was examined herein and identified as *E. izbus.*

Examined material. Non-type material: USA: 1♂ "Cleveland, S. C. July 28, 1971 G. Townes Family", 1♀ "Cleveland, S. C. August 3, 1971 G. Townes Family", 1♀ "Cleveland, S. C. August 8, 1971 G. Townes Family", and 1♀ "Cleveland, S. C. August 12, 1971 G. Townes Family" (USUC).

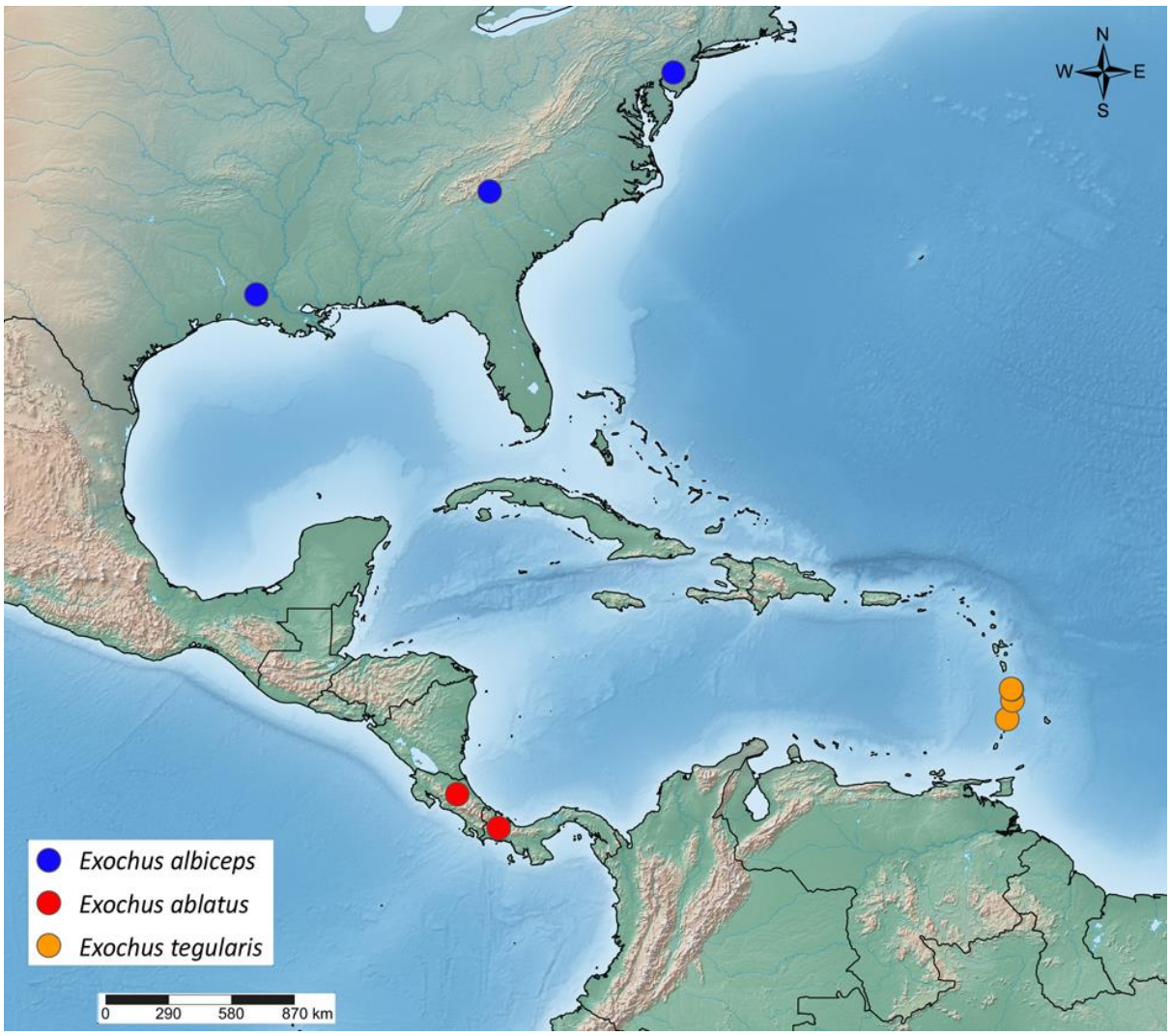

Figure 29. Localities of *E. ablatus*, *E. albiceps*, and *E. tegularis.*

***Exochus izbus* Gauld & Sithole 2002**

Exochus izbus Gauld & Sithole, 2002: 99

Figures 30, 31

Diagnosis. Face+clypeus 0.7–0.8× as long as wide; malar space 1.1–1.4× as long as basal mandibular width; antenna with 31–37 flagellomeres; mesopleuron with epicnemial carina complete, in some individuals preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.2–0.3× as long as length of vein Cu1 between M and Cu1; propodeum with median part black; metacoxa off white with a blackish longitudinal mark latero-externally; metatibia predominantly off white and dorsally brownish; metasoma black with lateral margin of tergites III–IV, in some individuals also distal margin, off white.

Distribution. This species was previously known only from Brazil (De Melo *et al*. 2015) and Costa Rica (Gauld & Sithole 2002); its distribution (Fig. 31) is expanded to include Argentina, Bolivia, Ecuador, French Guiana, Guatemala, Honduras, Mexico, Panama, Peru, Uruguay and Venezuela. This species occurs from southern Mexico to Argentina between sea level and 1,660 m.

Remarks. *Exochus izbus* was the most commonly collected metopiine in Costa Rica (Gauld & Sithole 2002), and also the most commonly encountered species of the *albiceps* species-group. This species was collected using light traps, malaise traps, yellow pan traps, and FITs. The records present here include first occurrence of the genus for Bolivia, Honduras, and Uruguay. There is no documented record of the Ichneumonidae for Uruguay, so this constitutes the first formal record of any member of this family for this country.

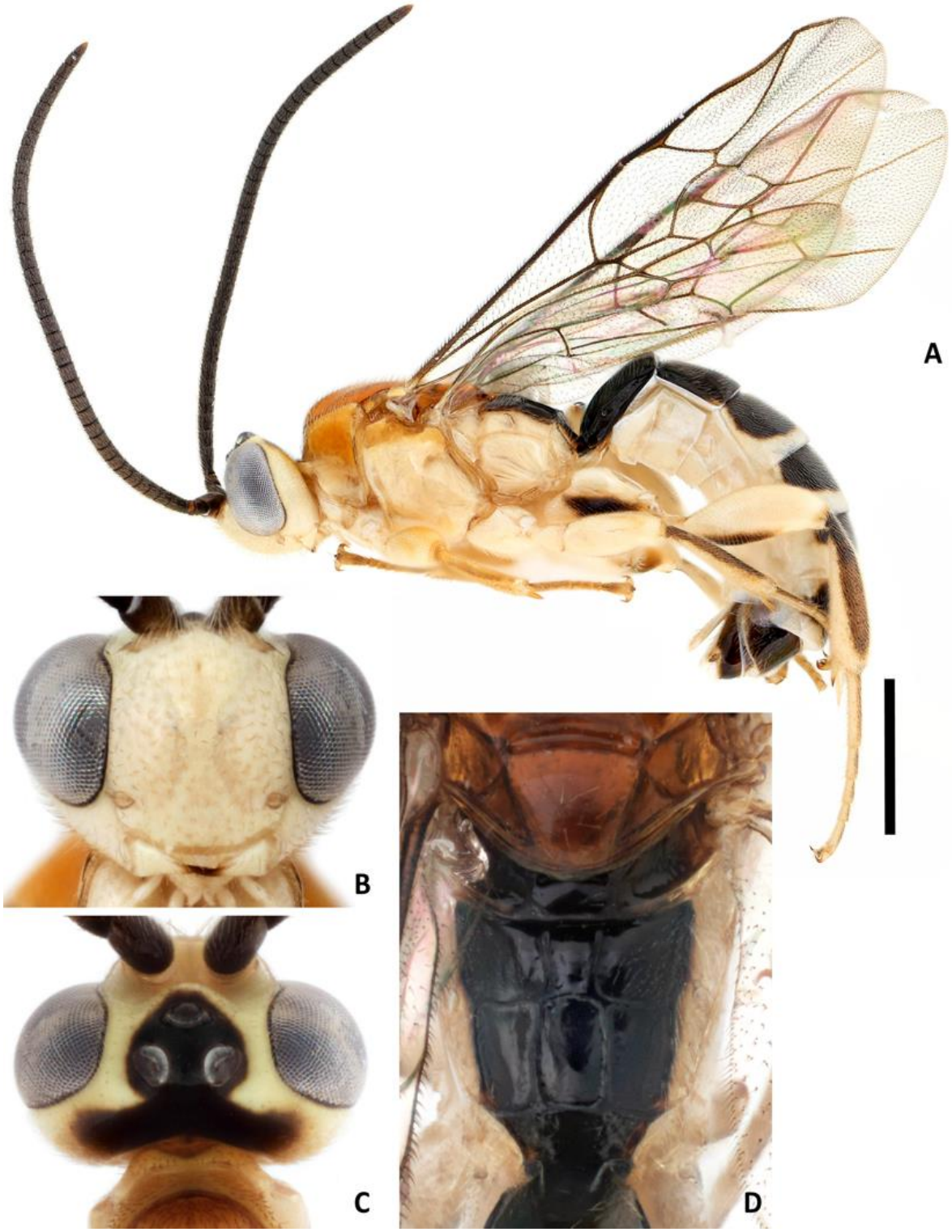

Figure 30. Morphology of *Exochus izbus* Gauld & Sithole, female (non-type). **A.** Lateral habitus (scale bar=1mm). **B.** Head, facial view. **C.** Dorsal view of head. **D.** Dorsal view of propodeum.

Examined material. Holotype: ♀ COSTA RICA: Guanacaste Prov., Guanacaste National Park, Estacion Cacao, 1000 m, vii.1988 Gauld & Janzen (MNCR). **Non-type material:**

ARGENTINA: ♀ “ARGENTINA: Misiones Loreto, Subtropical Wet Forest, X-XI-2003 C. Porter & P. Fidalgo Malaise trap” (FSCA). **BOLIVIA:** ♀ “Alto Beni, Bolivia S. Inicua R. 1100m I.15-18.76 L. Peña’, and, ♀ “BOLIVIA: Cochabamba 67.5 km NE Villa Tunari 17º6.52’S 64º48.87’W 300m, 9-13.ii.1999 R&S Hanley FIT [CNC493504]”(CNC). **BRAZIL:** ♀ “Jatai, Goias Jan.’77 Brazil F. M. Oliveira”, ♀, ♂ “Represa Rio Grande, Guanabara, Brazil August, 1966 M. Alvarenga”, ♀ “Represa Rio Grande, Guanabara, Brazil August, 1969 M. Alvarenga”, ♀ “Represa Rio Grande, Guanabara, Brazil December, 1969 M. Alvarenga”, ♀ “Represa Rio Grande, Guanabara, Brazil January, 1968 M. Alvarenga”, ♀ “Represa Rio Grande, Guanabara, Brazil March, 1970 M. Alvarenga”, 2♀♀ “Represa Rio Grande, Guanabara, Brazil May, 1967 M. Alvarenga”, ♀ “Represa Rio Grande”, ♀ “Guanabara, Brazil October, 1969 M. Alvarenga”, ♀, ♂ “Represa Rio Grande, Guanabara, Brazil September, 1966 M. Alvarenga”, 3♀♀ “Represa Rio Grande, Guanabra, Brazil VII.1966 M. Alvarenga”, 5♀♀ “Represa Rio Grande, VII.'72 Guan. Brazil M. Alvarenga”, and, ♀ “Margaratiba Muriqui R. d. J. VII.'69 Brazil M. Alvarenga” (USUC); ♂ “Nova Teutonia 27º11’S 52º23’W BRAZIL, 300-500m 2.1965 Fritz Plaumann[CNC493503]”, ♂ “Nova Teutonia 27º11’S 52º23’W BRAZIL, 300-500m XII.1968 Fritz Plaumann [CNC493502]” (CNC). **ECUADOR:** 2♀♀, ♂ “Coca & Napo Rivers V.1-12.65 Ecuador Luis Peña”, 2♀♀ “Coca, Ecuador May 1965 Luis Peña”, ♀ “ECU: Pich.; 250m 47km S Sto. Domingo Rio Palenque Sta. 22-27.ii.76 S. Peck”, ♀ “ECUADOR: Pichincha, Rio Palenque Science Centre, 0.6ºS, 79.35ºW, 800m; 2-3.iii.1996; P. Hibbs; Malaise trap”, 2♀♀ “47km. S. S. Domingo Pich. Pr., Ecuador II.17-25.79 L. Ling”, ♀ “San Lorenzo Esmer. Ecuador VI.3-10.75 5m. S. & J. Peck”, 2♂♂ “Sto. Domingo 700m Ecuador II.26.81 Henry Howden”, ♀ “ECUADOR: Sucumbios, Rio Napo, Sacha Lodge 0.5ºS, 76.5ºW, 290m; 1-31.xii.1994; P. Hibbs ♀ “ECUADOR: Sucumbios, Rio Napo, Sacha Lodge 0.5ºS, 76.5ºW, 290m; 3-13.vii.1994; P. Hibbs”, 2♀♀ “ECUADOR: Zamora Chinchipe, Rio Bombuscaro, 4.12ºS,

78.98ºW 1050m; 25.vi-4.vii.1996; P. Hibbs; Malaise trap (USUC); ♀ “Pompeya, Napo R. Pastaza, ECUAD. 14-22.V.1965 L. Peña [CNC493505]”, ♀ “ECUADOR Rio Palenque 21-25.II.1979 Malaise trap [CNC493506]”, ♀ “ECUADOR: Pichincha, 47km S. Santo Domingo Rio Palenque, 250m 5.v-25.vii.1985. S&J.Peck ex. Rainforest, FIT/MT [CNC493507]”, and, ♀ “ECUADOR: Pichincha, Maquipucuna biological satation, river trail, 0º7’34”N 78º37’57”W 27-29.x.1999 Z. Falin [CNC493508]” (CNC). **FRENCH GUIANA:** ♂ “FRENCH GUIANA: Saül 7 km N & 3 Km SE Les Eaux Claires. Mount Fumée, 490m, 1-8.vi.1997, J. Ashe & R. Brooks FIT#162 [CNC493510]”, ♀ “FRENCH GUIANA: PK35 4º32.663’N 52º09.371’W 230m 5.xii.2007, Malaise trap, rain forest, J. Cerda [CNC493511]”, and, ♀ “FRENCH GUIANA: Patawa, Kaw Mountain, viii.2008, Malaise trap, J. Cerda [CNC493512]” (CNC). **GUATEMALA:** 3♀♀ “GUATEMALA: Izabal, Las Escobas, 200m; vi.1987; M.J. Sharkey”, and, ♀ “GUATEMALA: Izabal, Las Escobas, 200m; v.1987; M.J. Sharkey” (USUC); ♀ “GUATEMALA: Izabal, Las Escobas, 300m, 22.iii.1987 M. Sharkey [CNC493269]” (CNC); and, 2♀♀ “GUATEMALA: Suchitepéquez; Volcán Atitlán, Ref. El Quetzal 1660m 14.55012 -91.19377 14-18-XI-2016 ZHFalin & FCarillo ex. Flight intercept trap, wet montane forest GUAT1F16 016.5 [SEMC1532046 and SEMC153198]” (SEMC). **HONDURAS:** ♀ “HONDURAS: Atlantica, Tela, Lancetilla Botanical Garden, 10-20 m; 23.vi.1994; J. Ashe & R. Brooks; #199”, and, ♀ “HONDURAS: Santa Barbara, La Fe, Finca La Roca, 740 m; 19-21.vi.1994; J. Ashe & R. Brooks” (USUC). **MEXICO:** ♂ “MEXICO: Chiapas, Laguna Belgica, 16 km NW Ocozocoautla; 14.vi.1990; H. Howden”, and, ♂ “MEXICO: Chiapas, Laguna Belgica, 16 km NW Ocozocoautla; 7.vi.1990; H. Howden” (USUC); 8♀♀, ♂ “MEXICO, Chiapas Muste, 440m. near Huixtla 21.ix.1970 Mal. Trap Welling”, ♀ “MEXICO: Veracruz, 33km NE Catemaco, Los Tuxtlas Biological Station, 160m, 1.vii-1.viii.1983 FIT J. & S. Peck, rain forest [CNC493270]”, and, 2♂♂ MEXICO: Chiapas, Musté, nr. Huixtla, 440m 11.x.1970 Malaise trap, Welling [CNC493271-

CNC493272]" (CNC). **PANAMA:** 4♀♀ "nr. HatoDelVolcan Panama 4700feet Jul.1982 B. Gill", ♀ "Panama ElLano-Carti Road July 1982 FIT 400m B. Gill", ♀ "PAN. B.C.I. Gatun L. IX-28-1982 H. Wolda", ♀, ♂ "PAN. B.C.I. Gatun L. VIII-15-1982 H. Wolda", ♂ "PAN. B.C.I. Gatun L. VIII-20-1982 H. Wolda", and, ♀ "Juan Gallegos Is. Canal Zona VI.'81 B. Gill" (USUC); ♀ "PANAMA: Chiriquí, 6km NE Boquete, 1650m, 14-19.vi.1996, FIT, J. Ashe & R. Brooks [CNC493268]" (CNC); and, ♂ "N. PANAMA: Fortuna (Chiriquí), 1050 m 8º44'N-82º15'W, 23-31.XII.1978, at light H.Wolda, RMNH'79", and ♀ "N. PANAMA: Fortuna (Chiriquí), 1050 m 8º44'N-82º15'W, 19-25.ix.1978, at light H.Wolda, RMNH'79" (NBCN). **PERU:** 1♀ "Perú: [Junín] La Merced Fundo Genova 19-24/03/2008 Tampa Malaise 1 AECID-/013484/07", 2♀♀ "Perú: La Merced Fundo Genova 19-24/05/2008 Tampa Malaise 1 AECID-/013484/07", 2♀♀ "Perú: La Merced Fundo Genova 24/05-07/06/2008 Tampa Malaise 1 AECID-/013484/07", ♀ "Perú: La Merced Fundo Genova 24/05-07/06/2008 Tampa Malaise 3 AECID-/013484/07", ♀ "Perú: La Merced Fundo Genova 02-23/08/2008 Tampa Malaise 1 AECID-/013484/07", ♀ "Perú: La Merced Fundo Genova 16-30/08/2008 Tampa Malaise 1 AECID-/013484/07", ♀ "Perú: La Merced Fundo Genova 30/08-13/09/2008 Tampa Malaise 1 AECID-/013484/07", 2♂♂ "Perú: La Merced Fundo Genova 13-27/09/2008 Tampa Malaise 1 AECID-/013484/07", ♀ "Perú: La Merced Fundo Genova 25/10-08/11/2008 Tampa Malaise 1 AECID-/013484/07"; 1♀ "Perú: La Merced Fundo Genova 07-22/12/2008 Tampa Malaise 1 AECID-/013484/07"; 1♀ "Perú: La Merced Fundo Genova 19-24/03/2008 Tampa Malaise 3 AECID-/013484/07"; ♀, ♂ "Perú: La Merced Fundo Genova 03-19/05/2008 Tampa Malaise 3 AECID-/013484/07"; 1♀ "Perú: La Merced Fundo Genova 07-21/06/2008 Tampa Malaise 3 AECID-/013484/07"; 2♀♀ "Perú: La Merced Fundo Genova 25/10-08/11/2008 Tampa Malaise 3 AECID-/013484/07"; 5♀♀, 2♂♂ "Perú: La Merced Fundo Genova 22/11-07/12/2008 Tampa Malaise 3 AECID-/013484/07"; 1♀ "Perú: La Merced Fundo Genova 07-22/12/2008 Tampa Malaise 3 AECID-

/013484/07”; 2♀♀ “Perú: La Merced Fundo Genova 19-24/03/2008 Tampa Malaise 2 AECID-/013484/07”; 3♀♀, 1♂ “Perú: La Merced Fundo Genova 19/04-03/05/2008 Tampa Malaise 2 AECID-/013484/07”; 1♀ “Perú: La Merced Fundo Genova 03-19/05/2008 Tampa Malaise 2 AECID-/013484/07”; 2♀♀ “Perú: La Merced Fundo Genova 19-24/05/2008 Tampa Malaise 2 AECID-/013484/07”; 2♀♀ “Perú: La Merced Fundo Genova 08-22/11/2008 Tampa Malaise 2 AECID-/013484/07”; 2♀♀ “Perú: La Merced Fundo Genova 22/11-07/12/2008 Tampa Malaise 2 AECID-/013484/07; 1♀ “Perú: La Merced Fundo Genova 22/12/2008-03/01/2009 Tampa Malaise 2 AECID-/013484/07”; 1♀ “Perú: La Merced Fundo Genova 03-17/01/2009 Tampa Malaise 2 AECID-/013484/07”; 2♀♀ “Perú: La Merced Fundo Genova 17-31/01/2009 Tampa Malaise 2 AECID-/013484/07”; 1♀, 1♂ “Perú: La Merced Fundo Genova 19-24/03/2008 Tampa Malaise 4 AECID-/013484/07”; 1♀ “Perú: La Merced Fundo Genova 19-24/05/2008 Tampa Malaise 4 AECID-/013484/07”; 1♀ “Perú: La Merced Fundo Genova 02-16/08/2008 Tampa Malaise 4 AECID-/013484/07”; 1♂ “Perú: La Merced Fundo Genova 16-30/08/2008 Tampa Malaise 4 AECID-/013484/07”; 1♀ “Perú: La Merced Fundo Genova 08-22/11/2008 Tampa Malaise 4 AECID-/013484/07”; 1♀ “Perú: La Merced Fundo Genova 22/12/2008-03/01/2009 Tampa Malaise 4 AECID-/013484/07”; 1♀ “Perú: La Merced Fundo Genova 17-31/01/2009 Tampa Malaise 4 AECID-/013484/07” (MERK). 1♀ “PERU: AM, Bagua CCNN. Tutumberos 5º20'2.9"S, 78º27'12.5"W, 366m, 17-18.iv.2015 L. Sulca”, 1♀ “PERU: CU, La Convención, Echarate, Comunidad Nueva Luz, 73º01'13" [W]/ 11º39'15.6"[S] 407m. 16.vii.2013 V. Borda”, 1♂ “PERÚ: CU[Cuzco], La Convención Echarate, San Martin de Pangoa, nr Rio Mantaro, 12º10'1.93"S/ 73º3'52.64"W 555m. 16-18.xii.2010. F. Meza”; 1♀ “PERÚ: CU, Reserva Comunal Amarakaeri, 70º57'3.65"W/ 12º46'31.24" S 309m. 27-29.v.2011. Malaise. B. Medina y L. Huerto”; 1♀ “PERU: MD, Reserva Comunal Amarakaeri, 70o57'56.9"W/ 13o5'45.68"S 578m, 21-22.v.2011 Malaise B. Medina y L. Huerto”, 1♀, 2♂♂ “PERÚ: MD

[Madre de Dios]. Manu, Rio Serjali 12º42'55.5"S/ 71º14'31.6"W 428m, 19-21.i.2011 J. Acosta"; 1♀ "PERU: MD. Tambopata, Explorer's Inn, 12º50'30"S/ 69º17'31.1"W 161m. 27.ix.2009 [Malaise trap] M. Alvarado"; 1♀ "PERU: MD [Madre de Dios] Tambopata NNRR [Reserva Nacional], Explorer's Inn Amazon lodge, 12º50'44.2"S/ 69º17'34.5"W 189m. 07-23.ii.2009 Malaise 4, L. Sulca y M. Alvarado"; ♂ "PERÚ: JU. Chanchamayo, Pichanaqui, San Miguel de Autiki, 10º48'16.59"S/ 74º49'33.40"W, 1464m, 02-07.vi.2014 E. Rázuri", 1♀ "PERÚ: PA. Parque Nacional Yanachaga Chemillen, estación biológica Paujil, 373m, 10o19'24.8"S 75o15'50"W, 30.ix-03.x.2015. M. Rodríguez", 1♀ "PERÚ: LO[Loreto]. Ucayali, Contamana, CCNN [Comunidad Nativa] Nueve de Octubre 7º42'47"S/ 75º9'59" W 153m. 17-19.ix.2011. L. Sulca"; ♂ "PERÚ: LO. Ucayali, Padre Marquéz, CCNN Roaboya 7º46'44"S/ 74º54'47"W 152m. 11-12.x.2011. L. Sulca"; 2♀♀ "PERÚ: LO. Ucayali, Padre Marquéz, CCNN [Comunidad Nativa] Santa Ana 7º52'4"S/ 75º30'59"W 224m. 10-11.x.2011. L. Sulca"; 2♀♀ "PERÚ: UC[Ucayali], Coronel Portillo, Calleria 73º42'58.65"W/ 08º23'10.92"S 255m. 12.x.2012 B. Medina" (MUSM); ♀ "Avispas, 400m., PERU Madre de Dios Dept. Sept. 12-20, 1962 L. E Pena" (CNC). **URUGUAY:** 1♂ "URUGUAY: Rocha, Don Bosco, 34º05'02.6"S/ 53º45'44.5"O, 28.i.2015, Malaise 2, bosque-campo, E. Castiglioni e eq., cols.", 4♀♀ "URUGUAY: Rocha, Don Bosco, 34º05'02.6"S/ 53º45'44.5"O, 28.i.2015, Malaise 1, bosque-campo, E. Castiglioni e eq., cols.", 1♀ "URUGUAY: Rocha, Don Bosco, 34º05'02.6"S/ 53º45'44.5"O, 26.ii.2015, Malaise 2, bosque-campo, E. Castiglioni e eq., cols.", 1♀ "URUGUAY: Rocha, Don Bosco, 34º05'02.6"S/ 53º45'44.5"O, 11.ii.2015, Malaise 2, bosque-campo, E. Castiglioni e eq., cols.", 1♀ "URUGUAY: Rocha, Don Bosco, 34º05'02.6"S/53º45'44.5"O, 12.1.2015, Malaise 1, bosque-campo, E. Castiglioni e eq., cols.", and 1♀ "URUGUAY: Rocha, Cardoso, 32º05'26.8"S/53º52'14.4"O, 11.ii.2015, Malaise 1, campo natural, Castiglioni e eq., cols." (INPA). **VENEZUELA:** ♀ "Venez.: Bolivar 8km. N of Guri VII.16-VIII.11.86 200m. B. Gill", ♀ "Venez.: Aragua Rancho

Grande VII.4-VIII.9.86 1150m B. Gill", ♀ "VENEZUELA: Aragua, Maracay, Rancho Grande 1200m; 1-10.VIII.1987 Bordon & Peck; flight intrcpt", ♀ "VENEZUELA: Aragua, Parque Nac. H. Pittier, Rancho Grande; 14-17.iv.1994; L. Masner", and, ♀ "Yacambú, Venez. 1200m V.7.81 H. K. Townes", ♂ "San Esteban, Ven. Nr. Puerto Cabello XII.20.1939 P. J. Anduze" (USUC); 2♀♀, ♂ "VENEZUELA: Aragua, Rancho Grande Biological Station, 26-28.ii.1995 FIT R. Brooks", ♀ "VENEZUELA: Aragua, Rancho Grande Biological Station, 10º21'N 67º41'W 14.v.1998 FIT J. Ashe, R. Brooks, R. Hanley [CNC493265]", ♀ "VENEZUELA: Aragua, Rancho Grande Biological Station, 1450m, 1-8.iii.1995 FIT #047 R. Brooks [CNC493266]", and, ♀ "VENEZUELA: Aragua, Rancho Grande Biological Station, 1140m, 1-6.iii.1995 FIT R. Brooks [CNC493267]" (CNC).

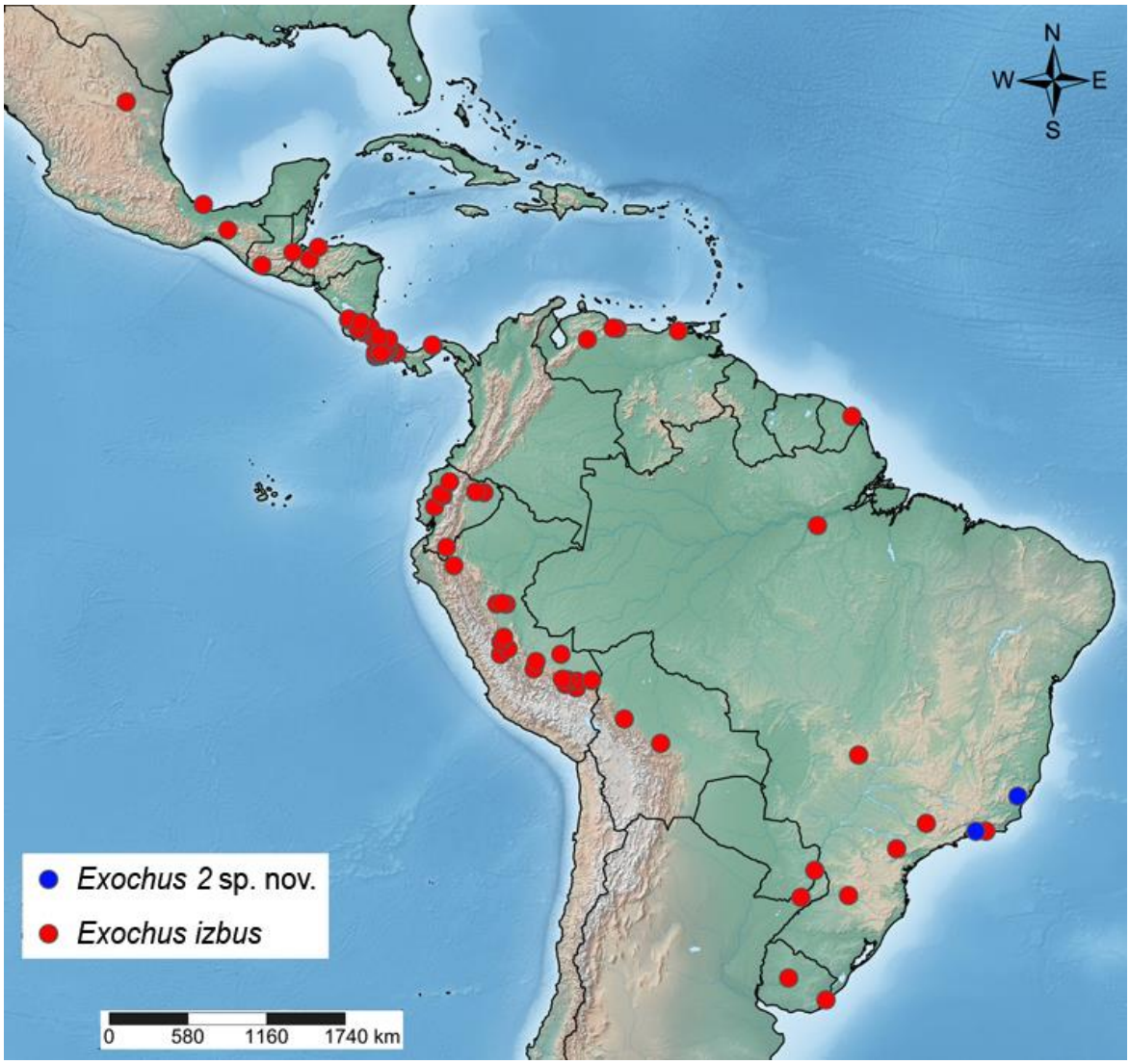

Figure 31. Localities of *E. izbus* and *Exochus* 2 sp. nov.

***Exochus jacintus* Gauld & Sithole 2002**

Exochus jacintus Gauld & Sithole, 2002: 102

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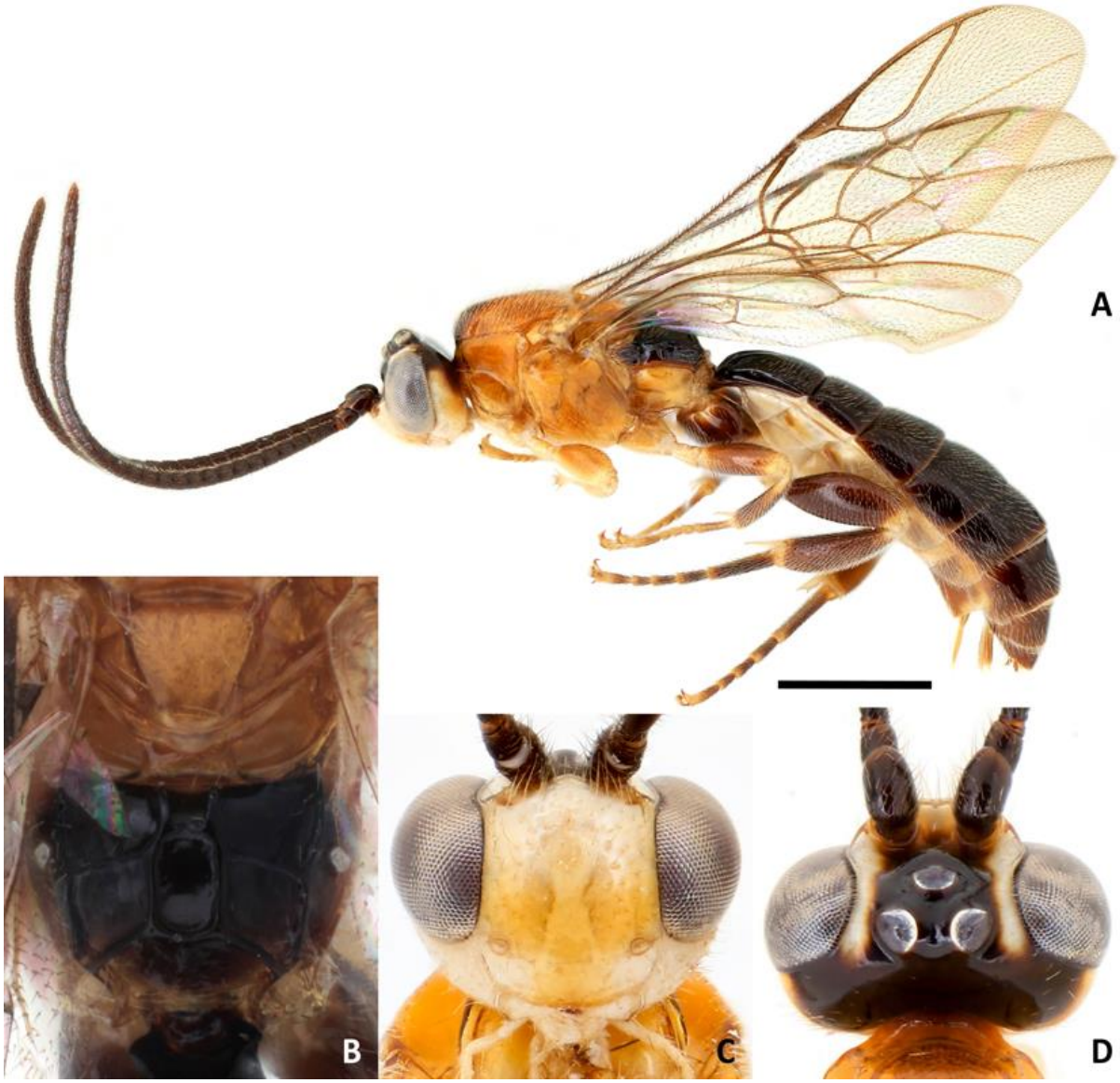

Figure 32. Morphology of *Exochus jacintus* Gauld & Sithole, female (non-type). **A.** Lateral habitus (scale bar=1mm). **B.** Dorsal view of propodeum. **C.** Head, facial view. **D.** Dorsal view of head.

Diagnosis. Face+clypeus 0.8× as long as wide; malar space 1.2–1.4× as long as basal mandibular width; antenna with 30–33 flagellomeres; mesopleuron with epicnemial carina preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.5–0.7× (rarely 0.4×) as long as length of vein Cu1 between M and Cu1, rarely 0.4×; propodeum blackish; metacoxal blackish, at most with apex off white; metatibia brown with extreme apex off white; metasoma black, in some individuals with apex brownish.

Distribution. This species was only known to occur in Costa Rica (Gauld & Sithole 2002). It occurs (Fig. 33) from Costa Rica to Paraguay; its distribution includes Brazil, French Guiana, Paraguay, Peru, Trinidad and Tobago, and Venezuela. It can be found in wet forest; the great majority was collected between sea level and 1,100 m and are less common between 1,100 and 1,500 m.

Remarks. This species was collected using Malaise traps, yellow pan traps, and FITs. This is the first record of the genus *Exochus* for Paraguay and Trinidad and Tobago.

Examined material. Non-type material: BRAZIL: 2♀♀ "Brazil: S. Paulo Gália Est. VII.84 F. M. Oliveira", 3♀♀ "Represa Rio Grande Guanabara, Brazil September, 1969 M. Alvarenga", 2♀♀ "Represa Rio Grande Guanabara, Brazil January, 1968 M. Alvarenga", 2♀♀ "Represa Rio Grande Guanabara, Brazil March 1972 M. Alvarenga", ♀ "Represa Rio Grande Guanabara, Brazil December, 1967 M. Alvarenga" and, ♀ "Represa Rio Grande Guanabara, Brazil December, 1969 M. Alvarenga" (USUC). **FRENCH GUIANA:** 4♀♀ "FRENCH GUIANA: 27 km SSE Roura, 240m 29.v-10.vi.1997 FIT J. Ashe & R. Brooks [CNC493273-CNC493276], ♀ "FRENCH GUIANA: Saül, pointe de vue du Belvedere, 1.5m 3º22'S 53o12'34" W 7.iii.2011 S.E.A.G. FIT [CNC493277]", and, ♀ "FRENCH GUIANA: 18.4 Km SSE Roura, 240m 29.v-10.vi.1997 J. Ashe & R. Brooks FIT#180 [CNC493278]" (CNC). **PARAGUAY:** ♀ "PARAGUAY: Itapua Yatai, San Rafael Rsv. 26o38'17"S

55o39'50"W 100m, 21-25.xi.2000 Z.H. Falin FIT" (CNC). **PERU:** 1♀ "Perú: La Merced Fundo Genova 22/12/2008-03/01/2009 Tampa Malaise 1 AECID-/013484/07"; 4♀♀ "Perú: La Merced Fundo Genova 03-17/01/2009 Tampa Malaise 3 AECID-/013484/07"; 2♀♀ "Perú: La Merced Fundo Genova 19-24/03/2008 Tampa Malaise 2 AECID-/013484/07";

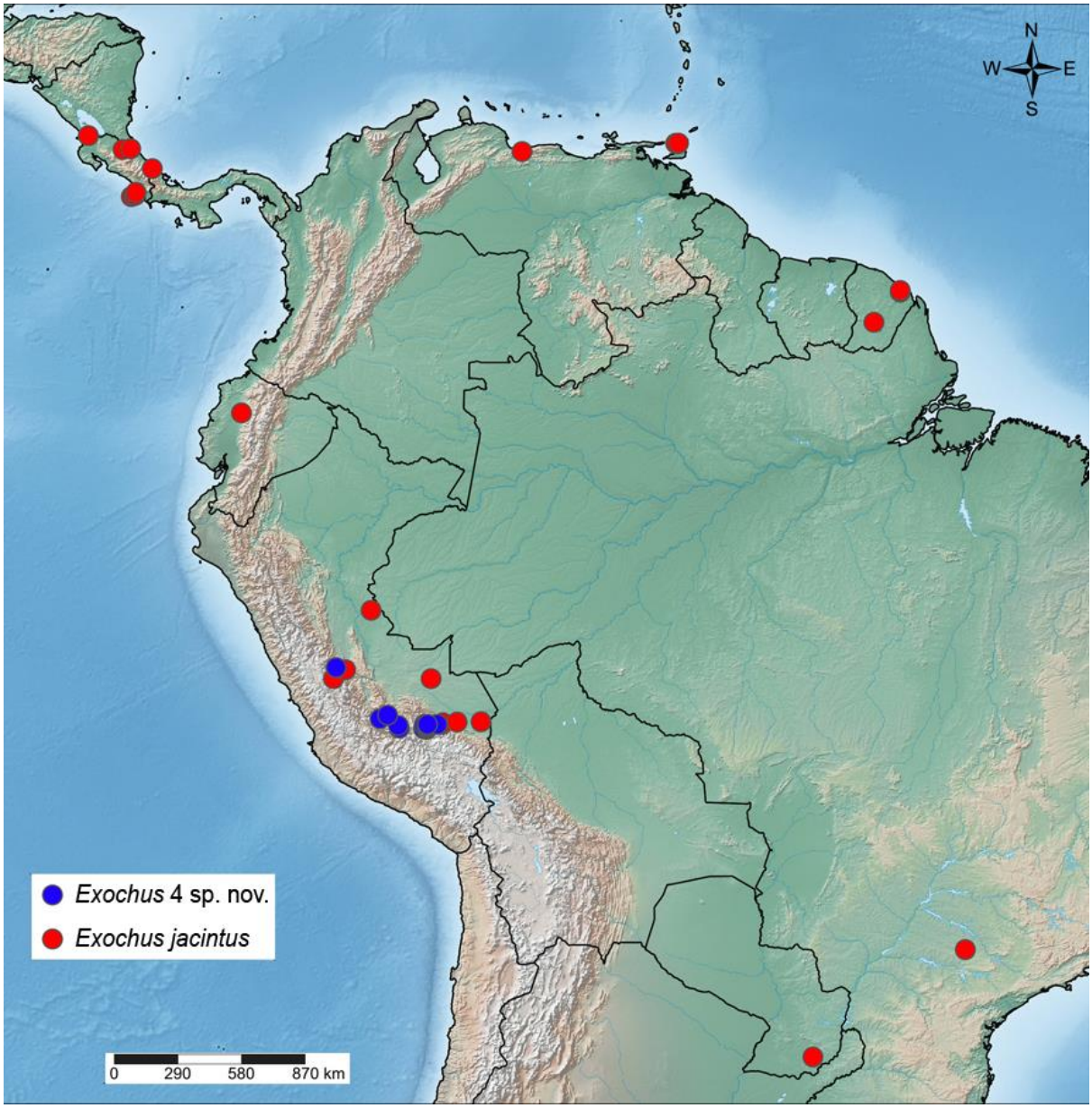

Figure 33. Localities of *E. jacintus* and *Exochus* 4 sp. nov.

1♀ "Perú: La Merced Fundo Genova 16-23/08/2008 Tampa Malaise 2 AECID-/013484/07"; 4♀♀ "Perú: La Merced Fundo Genova 22/12/2008-03/01/2009 Tampa Malaise 2 AECID-/013484/07"; and, 3♀♀ "Perú: La Merced Fundo Genova 22/12/2008-03/01/2009 Tampa Malaise 4 AECID-/013484/07" (MERK). 1♀ "PERÚ: CU, Cosñipata valley ca. P.V. Tono

13.xii.2007 12º56'50"S/ 71º31'55"W 865m, Malaise 16, C. Castillo"; 1♀ "PERÚ: CU, Reserva Comunal Amarakaeri, 13º01'20.79" S/ 70º55'12.34"W 774m. 04-06.xi.2010 [Yellow pan trap] C. Castillo"; 2♀♀ "PERÚ: CU, Reserva Comunal Amarakaeri, 13º0'3.88" S/ 70º50'32.59"W 864m. 10-14.xi.2010 [Malaise] C. Castillo"; ♀ "PERU: MD. Explorer's Inn Amazon lodge, 08.iii.2009 12º50'50"[S]/ 69º17'30"[W] 195 m Malaise 3, L. Sulca"; ♀ "PERÚ: JU. Chanchamayo, Pichanaqui, San Miguel de Autiki, 10º48'16.59"S/ 74º49'33.40"W, 1464m, 02-07.vi.2014 E. Rázuri", 2♀♀ "PERÚ: UC, Coronel Portillo, Calleria 73º42'58.65"W/ 08º23'10.92"S 255m. 12.x.2012 B. Medina" (MUSM). **TRINIDAD:** ♀ "TRINIDAD: 8 km N. Arima Simla Res. Station, 260m 14-24.vi.1993, lower montane rainforest, MT S. & J. Peck, 93-47 [CNC493280]", ♀ "TRINIDAD: 13km S Arima, 2km N Talporo, Quesmell farm, rainforest, FIT, 22.vi-8.vii.1993, 50m J. & S. Peck 93-46 [CNC493281], and, ♀ "TRINIDAD: Maracas 2-6.xii.1977 Malaise trap L.M. Mod [CNC493282]" (CNC). **VENEZUELA:** ♀ "VENEZUELA: Aragua, Henri Pittier National Park, Portachuelo Pass, 1000m 13.iv.1994 L. Masnier v94.3 [CNC493279]" (CNC).

***Exochus tegularis* Asmead 1894**

Exochus tegularis Asmead, 1894: 141

Figures 29, 34

Diagnosis. Face+clypeus 0.8–0.9× as long as wide; malar space 0.8–0.9× as long as basal mandibular width; antenna with 26–27 flagellomeres; mesopleuron with epicnemial carina well defined and ending at subalar prominence; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.2× as long as length of vein Cu1 between M and Cu1; propodeum with median part black; metacoxa off white with a blackish longitudinal mark

latero-externally; metatibia predominantly off white and dorsally brownish; metasoma black with lateral and distal margins tergites II–VII off white.

Redescription. Female: Forewing length 3.5–3.9 mm.

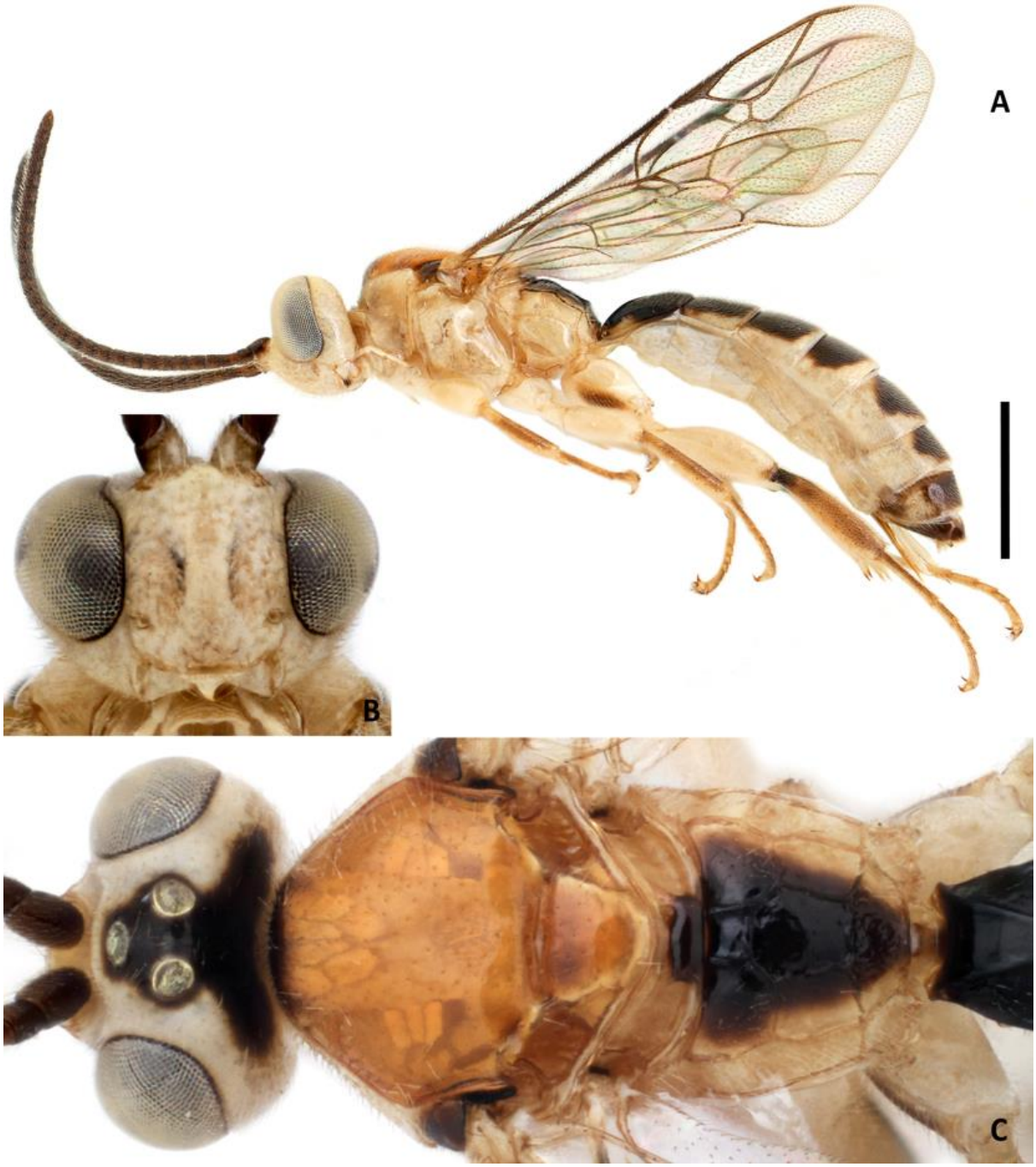

Figure 34. Morphology of *Exochus tegularis* Asmead, female (non-type). **A.** Lateral habitus (scale bar=1mm). **B.** Head, facial view. **C.** Dorsal view of head, mesoscutum, and propodeum.

Head. Face+clypeus 0.8× as long as wide (Fig. 34B); malar space 0.8–0.9× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.8–0.9× maximum ocellar diameter; distance between ocelli 1.0× maximum ocellar diameter (Fig. 34C); gena in lateral view 0.5–0.6× as long as compound eyes; antenna with 26–27 flagellomeres, ratio of length from second to fourth flagellomeres: 1.1–1.2:1.1:1.0.

Mesosoma. Mesopleuron with epicnemial carina ending at subalar prominence, complete (Fig. 34A). Submetapleural carina smooth, anteriorly expanded into triangular lobe. Propodeum (Fig. 34C) with anterior and posterior transverse carinae complete; lateromedian longitudinal present between base of propodeum and posterior transverse carina; lateral longitudinal carina present; area superomedia 1.0–1.3× as long as wide. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.5–0.6× its own length; Cu1 between 1m-cu and Cu1a 1.9–2.2× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.3–1.5× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.7–0.8× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of M not sclerotized; length of abscissa of Cu1 between Cu1 and 1A 0.2× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.6–0.7× as long as inner spur.

Metasoma. Tergite I 1.1–1.2× as long as posteriorly wide, lateromedian carinae extending 0.6× length of tergite; tergite II 0.6× as long as posteriorly wide; laterotergite II 0.2–0.3× as long as wide; laterotergite III 0.5–0.6× as long as wide, semicircular, mesal edge convex.

Color. Head mostly off white (Fig. 34B) with interocellar area and central part of occiput black (Fig. 34C). Mesosoma off white (Fig. 34A); mesoscutum tawny, anteriorly between notauli blackish; scutellum tawny; tegula, postscutellum and propodeum centrally black; legs off white, but femur ventrally, tibia dorsally, and tarsomeres dorsally brownish, metacoxa with blackish longitudinal mark latero-externally. Metasoma black with lateral and distal margins tergites II–VII off white.

Distribution. This species was known only from Saint Vincent; its distribution (Fig. 29) is expanded to the Caribbean islands of Martinique and Saint Lucia.

Remarks. *Exochus tegularis* is the only species of *Exochus* known to occur in the Caribbean; this is the first record of the subfamily, genus, and species for Martinique and Saint Lucia. Previously, only species of *Enicospilus* (Ophioninae) were known to these islands (Yu *et al*. 2012).

Examined material. Non-type material: Examined material: MARTINIQUE: 8♀♀ "MARTINIQUE: 2 Km NW Diamant 14º29.4'N 61º02.5'W 6-23.vii.2010 Thorn forest 80m Malaise trap J. Peck [CNC493241-CNC493248]"; and, 3♀♀, 4♂♂ "MARTINIQUE: 1 km E Diamant 14º28.7'N 61º00.6'W 6-23.vii.2010 Thorn forest 10m Malaise trap J. Peck [CNC493249-CNC493255]" (CNC). **SAINT LUCIA:** 3♀♀ "SAINT LUCIA: West Indies 14-21.v.1971, Univ. of Waterloo [CNC493256-CNC493258]" (CNC).

***Exochus* 1 sp. nov.**

Figures 35, 36

Diagnosis. Face+clypeus 0.8× as long as wide; malar space 1.3–1.4× as long as basal mandibular width; antenna with 37–40 flagellomeres; mesopleuron with epicnemial carina preapically interrupted; propodeum with anterior transverse carinae at least centrally well defined, area superomedia and dentipara not enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.7–0.8× as long as length of vein Cu1 between M and Cu1; propodeum tawny; metacoxa tawny; metatibia brown; metasoma black.

Description. Female: Forewing length 4.8 mm.

Head. Face+clypeus 0.8× as long as wide (Fig. 35C); malar space 1.5× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.7× maximum ocellar diameter; distance between ocelli 0.6× maximum ocellar diameter; gena in lateral view 0.6× as long as compound eyes (Fig. 35D); antenna with 37 flagellomeres, ratio of

length from second to fourth flagellomeres: 1.2:1.1:1.1, subapical flagellomere elongate, 1.2× as long as centrally broad, clearly longer than broad.

Mesosoma. Mesopleuron with epicnemial carina ending at subalar prominence, preapically interrupted (Fig. 35). Submetapleural carina smooth, anteriorly expanded into triangular lobe. Propodeum (Fig. 35B) with anterior transverse carina complete; posterior transverse carina absent centrally, faintly indicated next to lateral longitudinal carina (complete between lateral and pleural carinae); lateromedian longitudinal present between base of propodeum and posterior transverse carina; lateral longitudinal carina present; area superomedia not enclosed. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.4× its own length; Cu1 between 1m-cu and Cu1a 1.6× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.3× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.8× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of M sclerotized; length of abscissa of Cu1 between Cu1 and 1A 0.7× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.6× as long as inner spur.

Metasoma. Tergite I 1.4× as long as posteriorly wide, lateromedian carinae extending 0.8× length of tergite; tergite II 0.8× as long as posteriorly wide; laterotergite II 0.2× as long as wide; laterotergite III 0.5× as long as wide, semicircular, mesal edge convex.

Color. Head mostly yellow with occiput, interocellar area, median part of frons and upper half of gena black (Fig. 35D); antenna black. Mesosoma tawny (Fig. 35A); legs pale tawny with protibia dorsally, protarsomeres, and metafemur dorso-apically brownish; mesotibia dorsally, mesotarsomeres, metatibia, and metatarsomeres brown. Metasoma black.

Variation. The paratypes differs from the holotype in the following: forewing length 4.8–5.0 mm; malar space 1.3–1.4× as long as basal mandibular width; distance between ocelli 0.6–0.7× maximum ocellar diameter; antenna with 37–40 flagellomeres, ratio of length from second to fourth flagellomeres: 1.2:1.1–1.2:1.1, subapical flagellomere elongate, 1.1–1.2× as

long as centrally broad, clearly longer than broad; propodeum with anterior transverse carina complete or only present between lateromedian longitudinal carinae; forewing with crossvein 1cu-a distal to base of Rs&M about 0.4–0.5× its own length; Cu1 between 1m-cu and Cu1a 1.6–1.7× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.2–1.3× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.8–0.9× as long as abscissa of M between 2rs-m and 2m-cu; hind wing length of abscissa of Cu1 between Cu1 and 1A 0.7–0.8× as long as length of vein Cu1 between M and Cu1; tergite I with lateromedian carinae extending 0.7–0.8× length of tergite; tergite II 0.7–0.8× as long as posteriorly wide; laterotergite II 0.1–0.5× as long as wide; laterotergite III 0.5–0.6× as long as wide. Some individuals with metafemur ventro-anteriorly yellowish brown.

Male: Forewing length 4.9–5.3 mm. *Head.* Face+clypeus 0.8× as long as wide; lateral ocellus separated from compound eye by about 0.7–0.8× maximum ocellar diameter; distance between ocelli 0.6–0.8× maximum ocellar diameter; gena in lateral view 0.5–0.6× as long as compound eyes; antenna with 37–39 flagellomeres, ratio of length from second to fourth flagellomeres: 1.2–1.5:1.2–1.4:1.3–1.4, subapical flagellomere elongate, 1.2–1.4× as long as centrally broad, clearly longer than broad.

Mesosoma. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.6× its own length; Cu1 between 1m-cu and Cu1a 2.3× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.4–1.5× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.7× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.9× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.6–0.7× as long as inner spur.

Metasoma. Tergite I 1.4–1.5× as long as posteriorly wide, lateromedian carinae extending 0.7× length of tergite; tergite II 0.7× as long as posteriorly wide; laterotergite II 0.2× as long as wide; laterotergite III 0.6× as long as wide.

Figure 35. Morphology of *Exochus* 1 sp. nov., female. **A.** Lateral habitus (scale bar=1mm). **B.** Dorsal view of propodeum. **C.** Head, facial view. **D.** Dorsal view of head.

Color. Similar to female but legs pale tawny with metafemur dorsally brown and metatarsomeres white gradually changing in distal half to light brown.

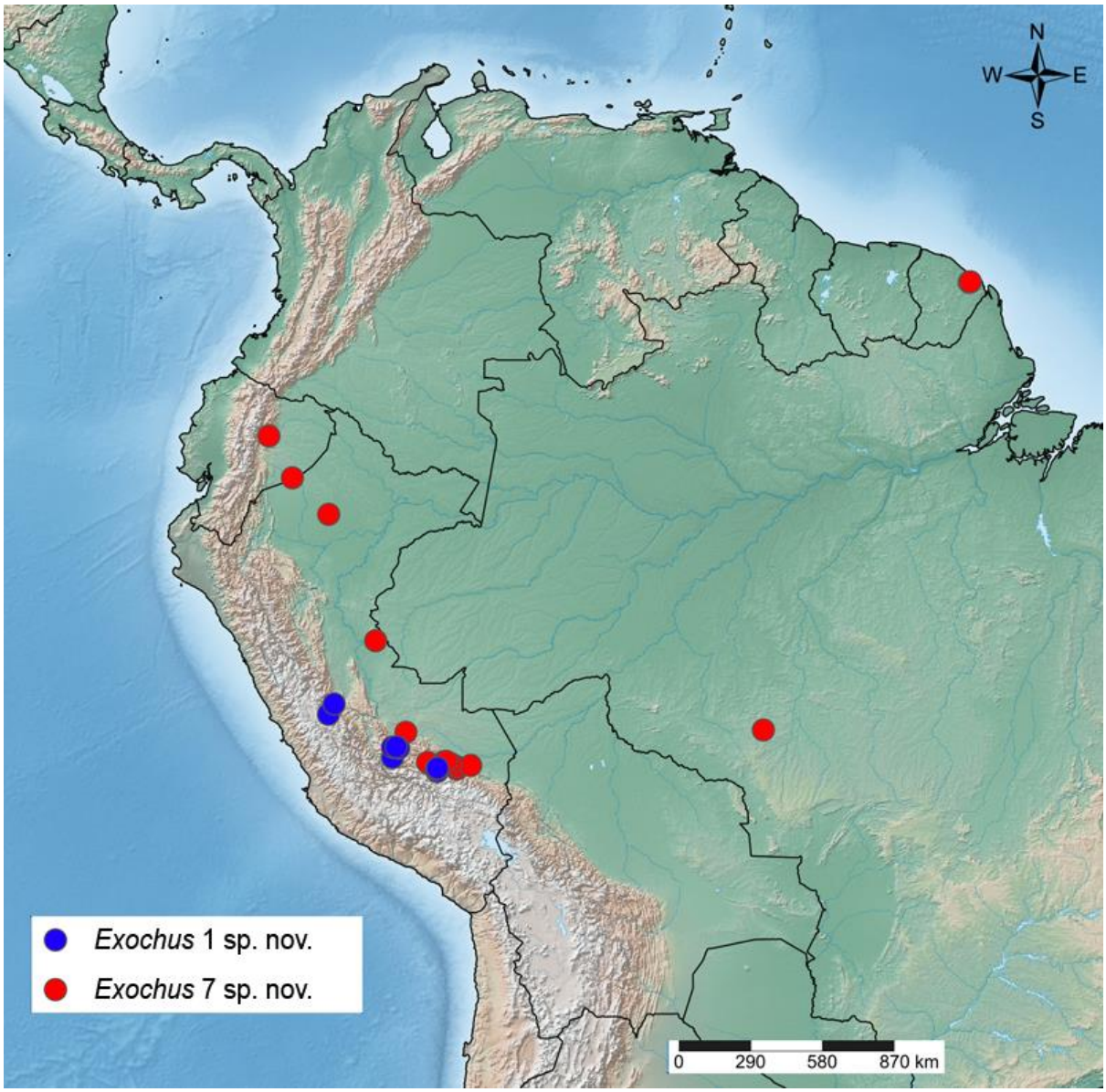

Figure 36. Localities of *Exochus* 1 sp. nov., and *Exochus* 7 sp. nov.

Male. Males differ from female in the following: face+clypeus 0.8–0.9× as long as wide; malar space 1.0× as long as basal mandibular width; gena in lateral view 0.4–0.5× as long as compound eyes; ratio of length from second to fourth flagellomeres: 1.5–1.6:1.5–1.6:1.4–1.5; propodeum with area superomedia 1.1–1.2× as long as wide. Tergite I 1.2× as long as

posteriorly wide, lateromedian carinae extending 0.6× length of tergite; tergite II 0.6–0.7× as long as posteriorly wide.

Male coloration similar to females except for mesoscutum extensively blackish, from blackish anteriorly between notauli and between lateral margin and notaulus to only tawny posterocentrally; mesoscutellum brownish.

Distribution. This species (Fig. 36) occurs in wet forest on the eastern slopes of the Peruvian Andes, between 861–1,734 m.

Remarks. This species was collected using Malaise traps, yellow pan traps, flight intercept traps (FIT), and manual netting.

Examined material. PERU: ♀ "PERU: CU. La Convención, Echarate, CC [Comunidad] Santa Rosa, 12º33'51.93"[S]/ 73º05'36.01"W 1434m. 18-21.ix.2010. MA [Malaise] M. Alvarado y J. Peralta", 1♀, "PERU: CU, La Convención, Reserva Comunal Matsigenga 12º13'33.81"S/73º02'06.98"W 1297m, 03.viii.2007, A. Asenjo / Premontane forest Yellow pan trap p9-y10" (metasoma and genitalia extracted and preserved in a glass vial), 1♂ "PERU: CU, La Convención, Reserva Comunal Matsigenga 12º13'37.2"S/73º01'59.7"W 1180m, 11.iii.2007, J. Santiesteban / Premontane forest Malaise trap P07-m5", 1♂ "PERU: CU, La Convención, Reserva Comunal Matsigenga 12º13'37.21"S/73º01'59.78"W 1180m, 1.viii.2007, A. Asenjo / Premontane forest Flight intercept trap P7-Mb02", 1♀, 3♂♂ "PERU: CU, La Convención, Reserva Comunal Matsigenga 12º13'37.21"S/73º01'59.78"W 1180m, 1.viii.2007, A. Asenjo / Premontane forest Malaise trap P07-m02" (males with metasoma and genitalia extracted and preserved in a glass vial), 2♀♀ "PERÚ: CU, Valle del Qosñipata, San Pedro. 13º03'11"S/ 71º32'08"W 08.xii.2007-08.i.2008. 1302m, Malaise trap 12 C. Castillo leg" (1♀ with metasoma and genitalia extracted and preserved in a glass vial), 1♀ "PERU: CU. La Convención, Echarate, CC. [Comunidad] Santa Rosa 12º33'55.00"S/73º05'37.35"W 1482m, 18-21.ix.2010. MA[Malaise] M. Alvarado y J. Peralta" (DNA extractions done), ♀

“PERU: CU. La Convención, Echarate, CC.PP. [Centro poblado] Tunquio72º52'34.21"W/ 12º15'39.33"S 1028m, 26/IX-01/X.2010 C. Carranza & S. Cavero”, ♀ “PERÚ: CU. Valle del Cosñipata, Tono 12º57'48"S/ 71º32'06"W xii.2007 862m. Malaise trap 15 C. Castillo”, ♀ “PERÚ: CU. Valle del Qosñipata, San Pedro 20.vi.2007 13º02'57"S/ 71º32'13"W 1500m. Manual C. Castillo”, ♀ “PERÚ: CU. Valle del Qosñipata, San Pedro. 13º02'58"S/ 71º32'13"W 20.ix.2007 1500m. Malaise trap C. Castillo leg”, ♀ “PERÚ: CU. Valle del Qosñipata, San Pedro. 13º03'25"S/ 71º32'25"W xii.2007 1520m. [Malaise trap] C. Castillo leg”, ♀ “PERÚ: CU. Valle del Qosñipata, San Pedro. 13º03'56.9"S/ 71º32'8.21"W 20.vii.2007 1500m. Malaise trap C. Castillo leg”, ♀ “PERÚ: JU. SN [Santuario Nacional] Pampa Hermosa 10º59'52.7"S/ 75º25'34.3"W 1757m. 30.v.2011 D. Silva leg” (left leg glued to cartoon board), ♀ “PERÚ: PA. Villa Rica, ZA [Zona de Amortiguamiento] del Bosque de Protección San Matias San Carlos 75º12'37"/10º38'44" 1596m. 6-10.viii.2012 Malaise trap P. Sanchez & E. Razuri” (molecular extractions done) MUSM.

***Exochus* 2 sp. nov.**

Figure 31, 37

Diagnosis. Face+clypeus 0.9× as long as wide; malar space 1.2× as long as basal mandibular width; antenna with 37–39 flagellomeres; mesopleuron with epicnemial carina preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.6× as long as length of vein Cu1 between M and Cu1; propodeum tawny; metacoxa tawny; metatibia brown; and metasoma brown gradually changing distally to tawny.

Description. Female: Forewing length 4.9 mm.

Head. Face+clypeus 0.9× as long as wide (Fig. 37B); malar space 1.2× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.8× maximum

ocellar diameter; distance between ocelli 0.8× maximum ocellar diameter (Fig. 37C); gena in lateral view 0.5× as long as compound eyes; antenna with 37 flagellomeres, ratio of length from second to fourth flagellomeres: 1.1:1.1:1.1, subapical flagellomere elongate, 1.1× as long as centrally broad.

Mesosoma. Mesopleuron (Fig. 37A) with epicnemial carina ending at subalar prominence, preapically interrupted. Submetapleural carina smooth, anteriorly expanded into triangular lobe. Propodeum with anterior and posterior transverse carinae complete; lateromedian longitudinal present between base of propodeum and posterior transverse carina; lateral longitudinal carina present; area superomedia 2.6× as long as wide. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.5× its own length; Cu1 between 1m-cu and Cu1a 1.9× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.3× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.7× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of M sclerotized; length of abscissa of Cu1 between Cu1 and 1A 0.6× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.6× as long as inner spur.

Metasoma. Tergite I 1.5× as long as posteriorly wide, lateromedian carinae extending 0.4× length of tergite; tergite II 0.8× as long as posteriorly wide; laterotergite II 0.3× as long as wide; laterotergite III 0.5× as long as wide, semicircular, mesal edge convex.

Color. Head (Figs. 37B, 37C) mostly yellow with occiput, interocellar area, median part of frons extensively and upper half of gena tawny; antenna black. Mesosoma tawny; proleg pale yellow; mesoleg pale yellow, distal 2/3 of tibia and tarsomeres brown; metaleg pale yellow, femur ventro and latero-distally brownish, tibia and tarsomeres brown. Metasoma (Fig. 37A) brown gradually changing distally to tawny.

Variation. The female paratype differs from the holotype in the following: malar space 1.4× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.7× maximum ocellar diameter; distance between ocelli 0.6× maximum ocellar diameter;

gena in lateral view 0.6× as long as compound eyes; antenna with 39 flagellomeres; propodeum with area superomedia 2.3× as long as wide; forewing with Cu1 between 1m-cu and Cu1a 1.6× as long as Cu1b, Cu1a between Cu1b and 2m-cu 1.2× as long as Cu1 between Rs&M and 1m-cu, 2rs-m 0.8× as long as abscissa of M between 2rs-m and 2m-cu; tergite I 1.4× as long as posteriorly wide; tergite II 0.7× as long as posteriorly wide; laterotergite III 0.6× as long as wide.

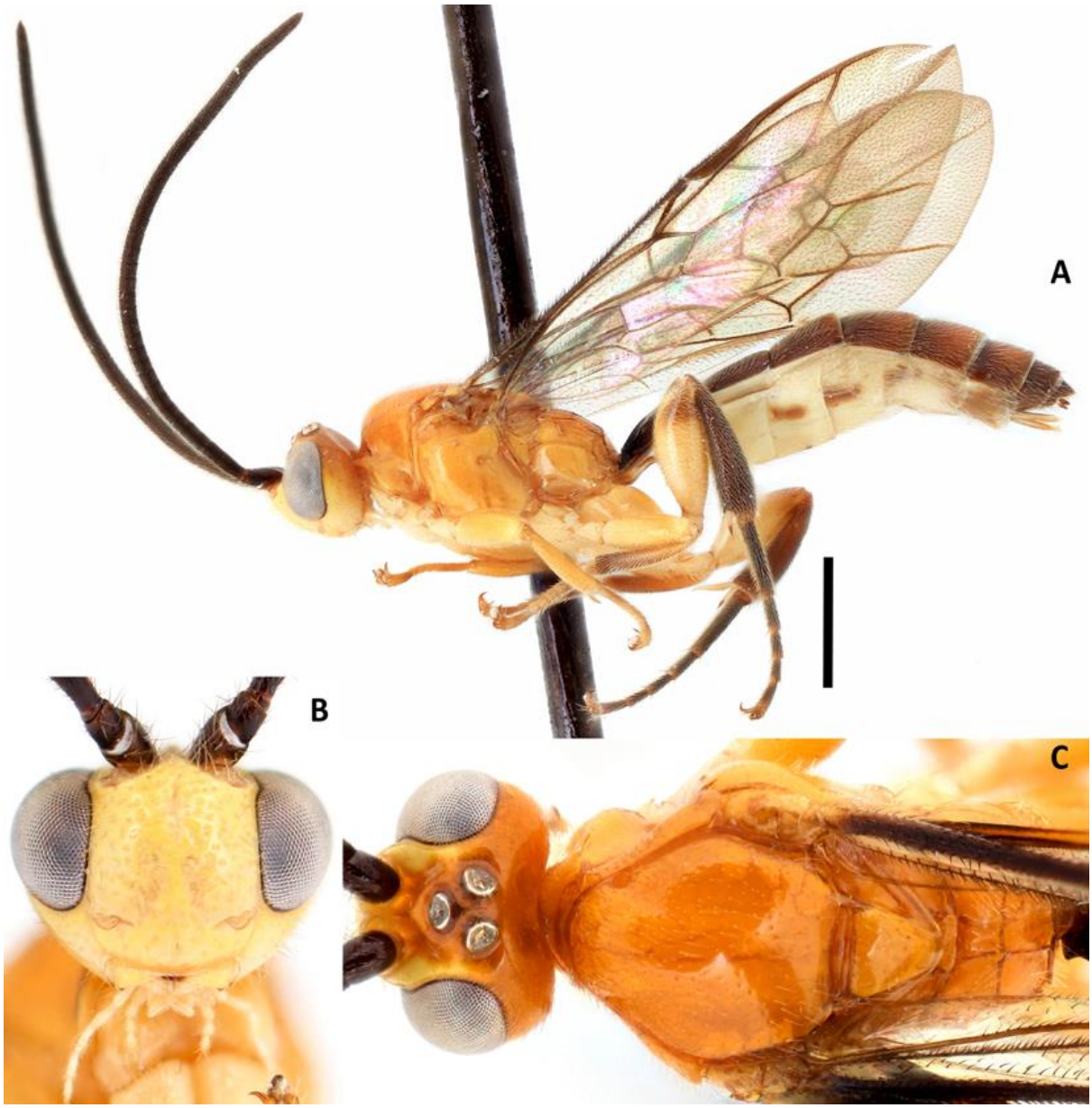

Figure 37. Morphology of *Exochus* 2 sp. nov., female. **A.** Lateral habitus (scale bar=1mm). **B.** Head, frontal view. **C.** Head in dorsal view, mesoscutum, and propodeum.

Male: Unknown.

Distribution. This species (Fig. 31) can be found in the Atlantic Forest in southeastern Brazil.

Examined material. BRAZIL: ♀, "Mangaratiba Muriqui [-22.9199,-43.9454] R.d.J. VII.'69 Brazil M. Alvarenga", and ♀, "Castelo, E. Santo [-20.5080,-41.4344] Nov.1976 Brazil M. Alvarenga" (USUC)

***Exochus* 4 sp. nov.**

Figures 33, 38, 39

Diagnosis. Face+clypeus 0.8× as long as wide; malar space 1.3–1.5× as long as basal mandibular width; antenna with 35–40 flagellomeres; mesopleuron with epicnemial carina preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.2–0.3× as long as length of vein Cu1 between M and Cu1; female with propodeum grading from entirely tawny to basal half brownish and metatibia tawny; male with propodeum predominantly black, metacoxa pale yellow with a blackish longitudinal mark ventrally; metatibia pale yellow but dorsally brown; metasoma, of both genders, black.

Description. Female: Forewing length 5.5 mm.

Head. Face+clypeus 0.8× as long as wide (Fig. 38B); malar space 1.5× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.7× maximum ocellar diameter; distance between ocelli 0.8× maximum ocellar diameter (Fig. 38C); gena in lateral view 0.6× as long as compound eyes; antenna with 37 flagellomeres, ratio of length from second to fourth flagellomeres: 1.1:1.1:1.1, subapical flagellomere elongate, 1.1× as long as centrally broad.

Figure 38. Morphology of *Exochus* 4 sp. nov., female. **A.** Lateral habitus (scale bar=1mm) **B.** Head, frontal view **C.** Dorsal view of head **D.** Dorsal view of propodeum.

Mesosoma. Mesopleuron with epicnemial carina ending at subalar prominence, preapically interrupted (Fig. 38A). Submetapleural carina smooth, anteriorly expanded into conspicuous semicircular lobe. Propodeum (Fig. 38D) with anterior and posterior transverse carinae

complete; lateromedian longitudinal present between base of propodeum and posterior transverse carina; lateral longitudinal carina present, faint between propodeum basally and anterior transverse carina; area superomedia 1.4× as long as wide. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.4× its own length; Cu1 between 1m-cu and Cu1a 2.6× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.6× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.7× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of M not sclerotized; length of abscissa of Cu1 between Cu1 and 1A 0.2× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.6× as long as inner spur.

Metasoma. Tergite I 1.6× as long as posteriorly wide, lateromedian carinae extending 0.5× length of tergite; tergite II 0.9× as long as posteriorly wide; laterotergite II 0.3× as long as wide; laterotergite III 0.6× as long as wide, semicircular, mesal edge convex

Color. Head mostly tawny with occiput brownish; interocellar area dark brown; lateral part of frons yellowish; antenna black. Mesosoma tawny (Fig. 38A); propodeum with area externa brownish; legs pale tawny. Metasoma black.

Variation. The female paratypes differ from the holotype in the following: forewing length 4.0–5.5 mm; malar space 1.3–1.5× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.7–0.8× maximum ocellar diameter; distance between ocelli 0.7–0.8× maximum ocellar diameter; antenna with 35–40 flagellomeres, ratio of length from second to fourth flagellomeres: 1.0–1.1:1.0–1.1:0.9–1.0, subapical flagellomere elongate, 1.1–1.2× as long as centrally broad; propodeum with area superomedia 1.6–2.2× as long as wide; forewing with crossvein 1cu-a distal to base of Rs&M about 0.4–0.6× its own length, Cu1 between 1m-cu and Cu1a 2.7–3.3× as long as Cu1b, Cu1a between Cu1b and 2m-cu 1.5–1.8× as long as Cu1 between Rs&M and 1m-cu, 2rs-m 0.8–1.0× as long as abscissa of M between 2rs-m and 2m-cu; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.2–0.3× as long as length of vein Cu1 between M and Cu1; tergite I

1.4–1.6× as long as posteriorly wide, lateromedian carinae extending 0.5–0.6× length of tergite; tergite II 0.8–0.9× as long as posteriorly wide; laterotergite II 0.1–0.4× as long as wide; laterotergite III 0.5–0.6× as long as wide.

There is considerable variation in the coloration of the species. Head mostly tawny with interocellar area extensively dark brown; some individuals with occiput centrally dark brown; or some individuals with a continuous dark brown mark from interocellar area to occiput; mesoscutum anteriorly between notauli brownish; propodeum from homogeneously tawny (Fig. 38D) to basal half brownish (Fig. 38A).

Male: Forewing length 4.4–6.3mm; *Head.* Face+clypeus 0.8× as long as wide; malar space 1.4–1.5× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.7–0.9× maximum ocellar diameter; distance between ocelli 0.6–0.8× maximum ocellar diameter (Fig. 39B); antenna with 36–39 flagellomeres, ratio of length from second to fourth flagellomeres: 1.4:1.4:1.4, subapical flagellomere elongate, 1.2–1.4× as long as centrally broad.

Mesosoma. Propodeum with area superomedia 1.5–1.8× as long as wide (Fig. 39C). Forewing with crossvein 1cu-a distal to base of Rs&M about 0.6× its own length; Cu1 between 1m-cu and Cu1a 2.2–2.4× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.4–1.5× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.7–0.8× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.2× as long as length of vein Cu1 between M and Cu1.

Metasoma. Tergite I 1.5–1.7× as long as posteriorly wide, lateromedian carinae extending 0.5–0.6× length of tergite; tergite II 0.9× as long as posteriorly wide; laterotergite II 0.1× as long as wide; laterotergite III 0.5× as long as wide.

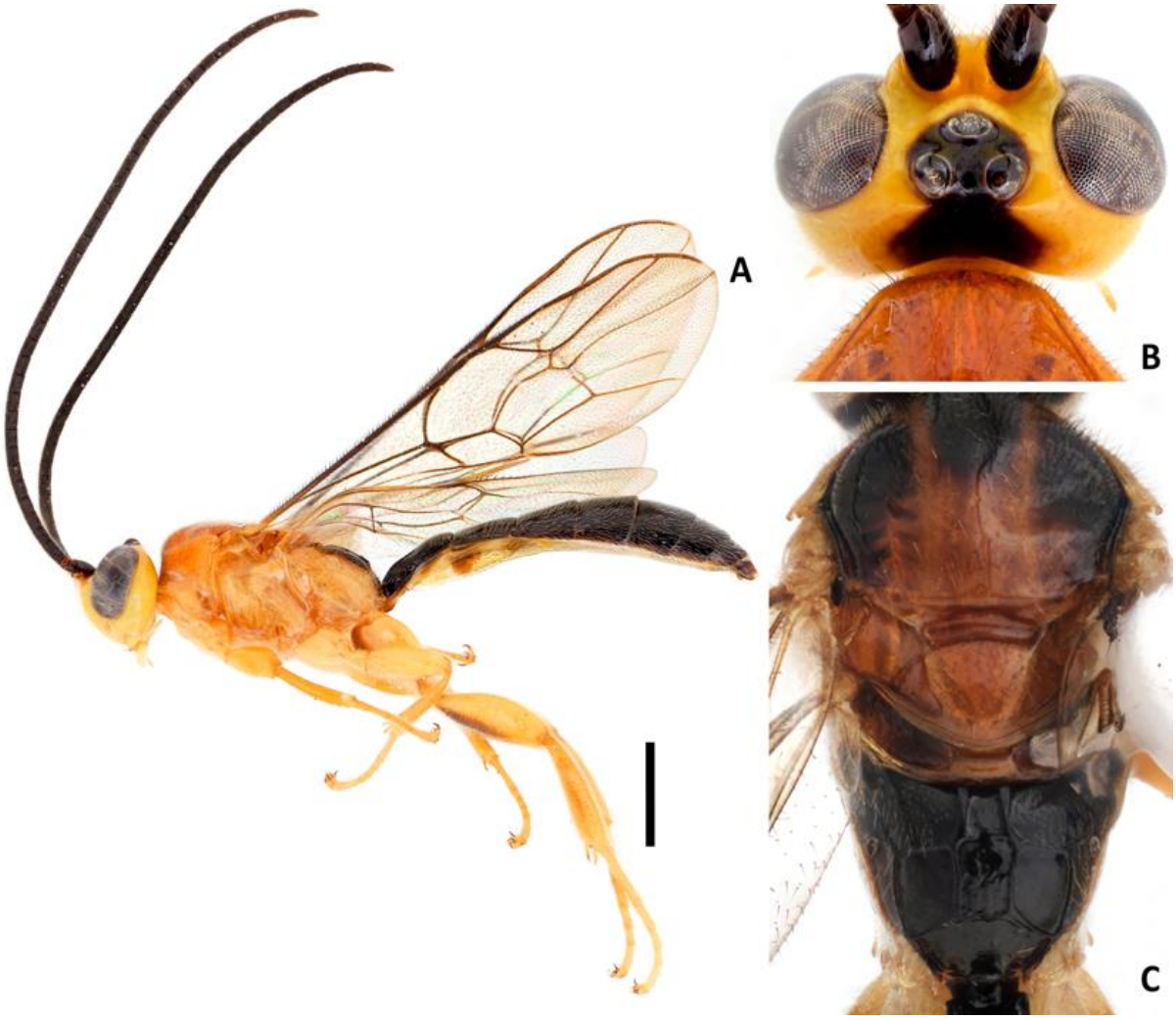

Figure 39. Morphology of *Exochus* 4 sp. nov., male. **A.** Lateral habitus (scale bar=1mm) **B.** Head, frontal view **C.** Mesoscutum, and propodeum.

Color. There is considerable variation in the coloration of the species. Head mostly pale yellow with occiput, interocellar area black, central part of frons may be entirely black, or entirely pale yellow or black with transverse pale yellow; antenna black. Mesosoma with pronotum and mesopleuron pale yellow; mesoscutum may be entirely tawny, or tawny with blackish marks laterally and centro-basally (Fig. 39C); scutellum, postscutellum and metanotum tawny; propodeum black (Fig. 39C), some individuals with area coxalis pale yellow; pro- and meso leg pale yellow; metaleg pale yellow with coxa and femur ventrally, trochantellus, and tibia dorsally brown, some individuals with tibia homogeneously pale yellow. Metasoma black.

Distribution. This is a widespread species (Fig. 33) in mid elevation at the eastern slopes of Peru, between 1,302–2,875 m. The great majority have been collected between sea level and 2,600–2,875 m and are less common between 1,300–2,300 m.

Remarks. This species was collected using Malaise traps, yellow pan traps, FITs, and manual netting.

Examined material. PERU: ♀ "PERÚ: CU, Wayquecha CC.II. [Centro de Investigación] 13º11'25.4"S/ 71º35'18.6"W 2664m. 21.vii.2007. Malaise trap C. Castillo leg", 2♀♀ "PERÚ: Cusco Dept., Wayqecha Field Station, cafeteria ~1km west research plot 13.17603º S 71.59481ºW, 2830m, 10-12.V.2011 DJ Bennett & E Razuri, Malaise trap, PER-11-MAT-002 [SEMC1037318, SEMC1037320]" (SEMC); 2♀♀ "PERÚ: CU. Wayquecha, CC.II. [Centro de Investigación] 13º10'40.6"S/ 71º35'2,06"W 09.xii.2007. 2874m, Malaise trap C. Castillo Leg", 2♀♀ "PERÚ: CU, Valle del Qosnipata [Qosñipata] C.I. Wayquecha 13º10'41"S/ 71º35'02"W 05.i.2008. 2874m, Malaise trap 6 C. Castillo", 1♀ "PERÚ: CU, C.I. 13o11'21"S/ 71o35'05"W 08.xii.2007-05.i.2008. 2865m, Malaise trap 7 C. Castillo leg", 1♀ "PERÚ: CU, C.I. Wayquecha 13º11'21"S/ 71º35'05"W 11.xi-08.xii.2007. 2865m, Malaise trap 7 C. Castillo leg", 1♀ "PERÚ: CU, C.I. Wayquecha 13º11'21"S/ 71º35'05"W 11.xi-08.xii.2007. 2865m, Malaise trap 7 C. Castillo leg", 1♀, 3♂♂ "PERÚ: CU, C.I. Wayquecha 13º11'21"S/ 71º35'05"W 20.x-11.xi.2007. 2865m, Malaise trap 7 C. Castillo leg", 5♀♀, 5♂♂ "PERÚ: CU, Wayquecha CC.II. 13º11'21.5"S/ 71º35'5.11"W 2865m. 20.x.2007. Malaise C. Castillo", 3♀♀, 1♂ "PERÚ: CU, Wayquecha C.I. 13º03'20.9"S/ 71º35'4.08"W 05.i.2008. 2837m, Malaise trap C. Castillo leg", 1♀, 1♂ "PERÚ: CU, C.I. Wayquecha 11.ix.2007 2800m 13º11'S/ 71º35'W Manual C. Castillo", 1♀ "PERÚ: CU. Wayquecha CC.II. 13º10'31.4"S/ 71º34'53.3"W 2692m. 09.xii.2007 Malaise trap C. Castillo leg", 2♂♂ "PERÚ: CU. Wayquecha CC.II. 13º10'31.4"S/ 71º34'53.3"W 2692m. 10.ix.2007 Malaise trap C. Castillo leg", 1♀ "PERÚ: CU. Wayquecha CC.II. 13º10'31.4"S/ 71º34'53.3"W 2692m. 21.x.2007

Malaise trap C. Castillo leg", 1♀ "PERÚ: CU, C.I. Wayquecha 13º10'31"S/ 71º34'53"W 06.i.2008. 2692m, Malaise trap 5 C. Castillo leg", 5♀♀, 2♂♂ "PERÚ: CU, C.I. Wayquecha 13º10'31"S/ 71º34'53"W 11.ix.2007. 2692m, Malaise trap 5 C. Castillo leg" (1♀ with metasoma and genitalia extracted and preserved in a glass vial), 1♂ "PERÚ: CU, C.I. Wayquecha 13º10'31"S/ 71º34'53"W 14.ix.2007. 2692m, Malaise trap 5 C. Castillo leg", 3♂♂ "PERÚ: CU, C.I. Wayquecha 13º10'31"S/ 71º34'53"W 22.x.2007. 2692m, Malaise trap 5 C. Castillo leg", 3♂♂ "PERÚ: CU. Wayquecha CC.II. 13º10'31.4"S/ 71º34'53.3"W 2692m. 09.xii.2007 Malaise trap C. Castillo leg", 1♂ "PERÚ: CU, C.I. Wayquecha 13º03'21"S/ 71º35'04"W 08.xi-08.xii.2007. 2664m, Malaise trap 4 C. Castillo leg", 1♀ "PERÚ: CU, C.I. Wayquecha 13º03'21"S/ 71º35'04"W 13.ix.2007. 2664m, Malaise trap 4 C. Castillo leg", 2♀♀, 11♂♂ "PERÚ: CU, C.I. Wayquecha 13º03'21"S/ 71º35'04"W 20.x.2007. 2664m, Malaise trap 4 C. Castillo leg" (1♂ with metasoma and genitalia extracted and preserved in a glass vial), 1♀ "PERÚ: CU, Wayquecha CC.II. 13º11'25.4"S/ 71º35'18.6"W 2664m. 21.vii.2007. Malaise trap C. Castillo leg", 1♀ "PERU: CU, Paucartambo, Kosñipata, Wayqecha, intersection Trocha Oso with Trocha Mariposa, 2533 m, 13º09'57.9"S, 71º35'22.3"W, 31.x.2017, cloud forest, flight interception trap, M. Rodríguez & L. Pérez leg." (molecular extractions done), 2♂♂ "PERÚ: CU. Wayquecha CC.II. 13º11'25"S/ 71º35'18"W 2664m.12.ix.2007. [Malaise] C. Castillo", 1♀ "PERU: CU, Wayrapata Camp, 2320m 12º51'S/73º30'W, 11.viii.1998, Flight intercep trap, Camisea project / WA04.0811 Mp02", 1♂ "PERÚ: CU. Qosnipata, San Pedro. 13º03'10.7"S/ 71º32'8.31"W 1520m. 12.xii.2007 Malaise trap C. Castillo Leg", 2♀♀ "PERÚ: CU. Qosnipata, 13º03'22.5"S/ 71º32'55.2"W 1520m. 12.x.2007 Malaise trap C. Castillo leg", 1♂ "PERÚ: CU. Qosnipata, San Pedro, 13º03'10.7"S/ 71º32'8.31"W 1520m. 12.xii.2007 Malaise trap C. Castillo leg", 1♀ "PERÚ: CU. Qosñipata Valley, San Pedro. 13º2'59"S/ 71º32'13"W 1500m. 23.vii.2007 Malaise trap 1500 C. Castillo", 3♀♀, 1♂ "PERÚ: CU. Valle del Qosñipata, San Pedro.

13º02'58"S/ 71º32'13"W 20.ix.2007 1500m. Malaise trap C. Castillo leg", 1♀, 5♂♂ "PERÚ: CU, Valle del Qosñipata, San Pedro. 13º03'11"S/ 71º32'08"W 08.xii.2007-08.i.2008. 1302m, Malaise trap 12 C. Castillo leg", 1♂ "PERU, CU, La Convención, Echarate, CC. [Comunidad] Santa Rosa 12º33'55.00"[S] /73º05'37.35" [W] 1482m, 18-21.ix.2010. MA [Malaise] M. Alvarado y J. Peralta", 1♂ "PERÚ: CU, La Convención, Santa Teresa 13º2'32.42"S/ 72º38'43.90"W 2094m 13.xii.2014 J. Suarez", 1♀ "PERÚ: CU, Urubamba, Santa Teresa 13º10'22.50"S/ 72º33'56.30"W 1874m 13-14.xi.2014 I. Medina", 2♂♂ "PERÚ: PA. Villa Rica, ZA [Zona de Amortiguamiento] del Bosque de Protección San Matias San Carlos 75º12'37"[S]/10º38'44"[W] 1596m. 6-10.viii.2012 Malaise trap P. Sanchez & E. Razuri" (1♂ with metasoma and genitalia extracted and preserved in a glass vial), 2♂♂ "PERÚ: PA. Villa Rica, ZA [Zona de amortiguamiento] del Bosque de Protección San Matias San Carlos 75º12'37"[W]/ 10º38'44"1596m. 6-10.viii.2012 Yellow trap P. Sanchez & E. Razuri" (MUSM).

***Exochus* 5 sp. nov.**

Figures 40, 41, 44

Diagnosis. Face+clypeus 0.8× as long as wide; malar space 1.4–1.7× as long as basal mandibular width; antenna with 33–34 flagellomeres; mesopleuron with epicnemial carina preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.5–0.7× as long as length of vein Cu1 between M and Cu1; propodeum tawny; metacoxa tawny; metatibia dark brown; metasoma dark brown.

Description. Female: Forewing length 4.2 mm.

Head. Face+clypeus 0.8× as long as wide (Fig. 40C); malar space 1.7× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.6× maximum

ocellar diameter; distance between ocelli 0.7× maximum ocellar diameter; gena in lateral view 0.5× as long as compound eyes; antenna with 34 flagellomeres, ratio of length from second to fourth flagellomeres: 1.2:1.1:1.1, subapical flagellomere elongate, 1.3× as long as centrally broad.

Figure 40. Morphology of *Exochus* 5 sp. nov., female. **A.** Lateral habitus (scale bar=1mm). **B.** Dorsal view of head, and mesoscutum. **C.** Head, facial view. **D.** Dorsal view of propodeum.

Mesosoma. Mesopleuron with epicnemial carina ending at subalar prominence, preapically interrupted. Submetapleural carina smooth, anteriorly expanded into conspicuous

semicircular lobe. Propodeum (Fig. 40D) with anterior and posterior transverse carinae complete; lateromedian longitudinal present between base of propodeum and posterior transverse carina; lateral longitudinal carina present, faint between propodeum basally and anterior transverse carina; area superomedia 2.0× as long as wide. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.4× its own length; Cu1 between 1m-cu and Cu1a 1.5× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.1× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 0.7× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of M sclerotized; length of abscissa of Cu1 between Cu1 and 1A 0.5× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.7× as long as inner spur.

Metasoma. Tergite I 1.3× as long as posteriorly wide, lateromedian carinae extending 0.6× length of tergite; tergite II 0.6× as long as posteriorly wide; laterotergite II 0.2× as long as wide; laterotergite III 0.5× as long as wide, semicircular, mesal edge convex.

Color. Head mostly pale yellow with occiput (Fig. 40B), interocellar area, median part of frons and upper half of orbits near gena black; antenna black. Mesosoma tawny (Fig. 40A); protibia dorsally, protarsomeres dorsally brownish; mesofemur, mesotibia, mesotarsomeres, metafemur, metatibia and metatarsomeres dark brown. Metasoma dark brown.

Variation. The female paratypes differ from the holotype in the following: forewing length 4.0–5.0mm; malar space 1.4–1.5× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.6–0.8× maximum ocellar diameter; distance between ocelli 0.7–0.8× maximum ocellar diameter; gena in lateral view 0.5–0.6× as long as compound eyes; antenna with 33–34 flagellomeres, ratio of length from second to fourth flagellomeres: 1.2:1.1:1.1, subapical flagellomere elongate, 1.1–1.3x as long as centrally broad; propodeum with area superomedia 1.7–1.9× as long as wide; forewing with crossvein 1cu-a distal to base of Rs&M about 0.5× its own length, Cu1 between 1m-cu and Cu1a 1.5–1.8× as long as Cu1b, Cu1a between Cu1b and 2m-cu 1.1–1.2× as long as Cu1 between

Rs&M and 1m-cu, 2rs-m 0.5–0.8× as long as abscissa of M between 2rs-m and 2m-cu; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.5–0.7× as long as length of vein Cu1 between M and Cu1; outer metatibial spur 0.6–0.7× as long as inner spur; tergite I 1.2–1.3× as long as posteriorly wide, lateromedian carinae extending 0.5–0.6× length of tergite; tergite II 0.5–0.6× as long as posteriorly wide; laterotergite II 0.2–0.5× as long as wide; laterotergite III 0.5–0.6× as long as wide.

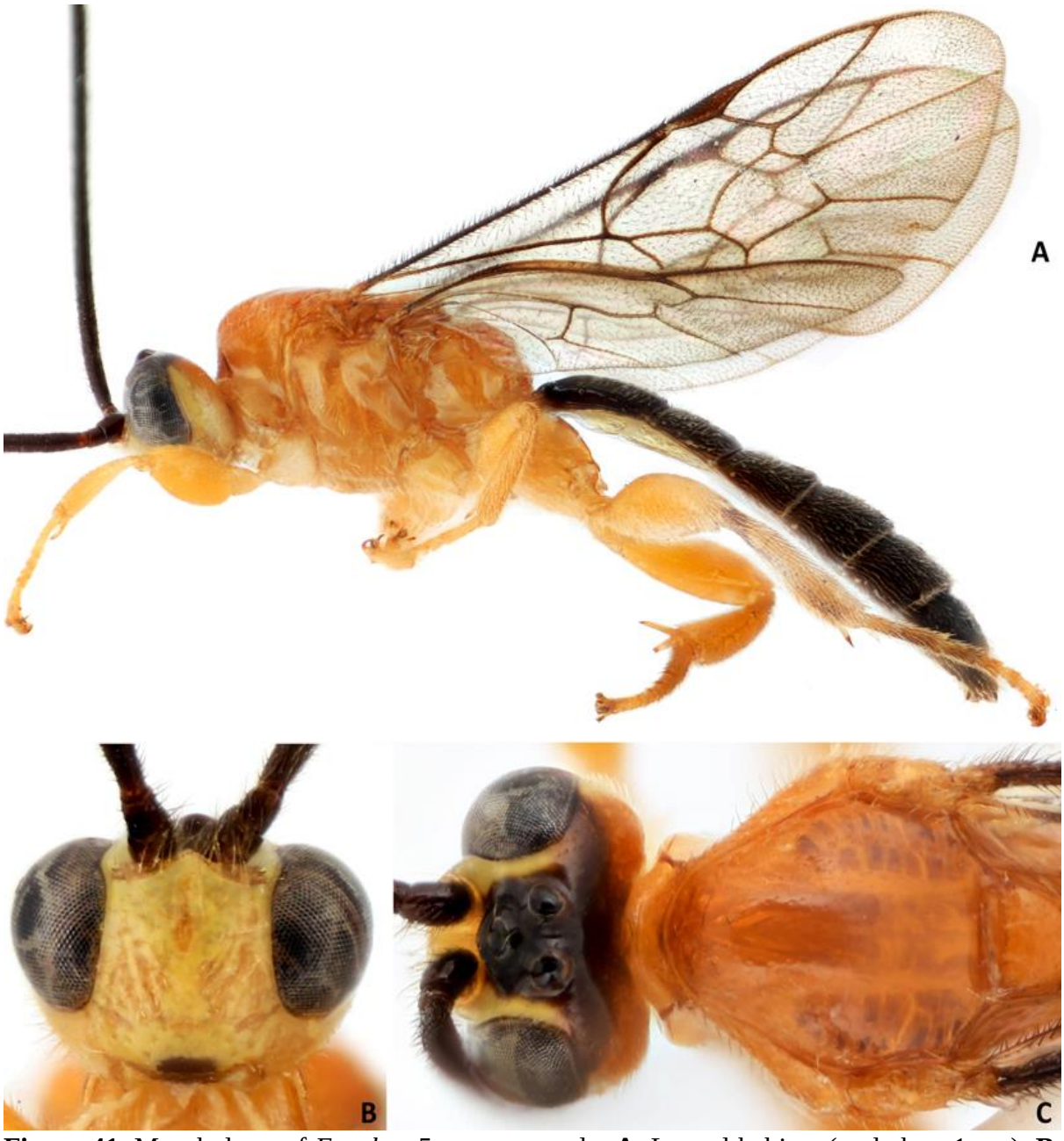

Figure 41. Morphology of *Exochus* 5 sp. nov., male. **A.** Lateral habitus (scale bar=1mm). **B.** Head, facial view. **C.** Dorsal view of head, and mesoscutum.

Male: The male paratype differs from the holotype in the following: distance between ocelli 0.9× maximum ocellar diameter; ratio of length from second to fourth flagellomeres: 1.4:1.4:1.4; subapical flagellomere elongate, 1.5× as long as centrally broad.

Coloration of the male is similar to that of females (Fig. 41A), except for having occiput with anterior half black and posterior half tawny (Fig. 41C), and clypeus with black next to margin (Fig. 41B); legs tawny with metatibia laterodorsally and metatarsomeres brownish (Fig. 41A).

Distribution. The species occurs (Fig. 44) in wet forest between see level to 1,100 m, in Bolivia, French Guiana, Surinam, and Peru.

Remarks. This species was collected using Malaise traps, yellow pan traps, and FITs.

Examined material. BOLIVIA: 1♀ "Alto Beni, Bolivia S. Inicua R. 1100m I.15-18.76 L. Peña" (USUC). **FRENCH GUIANA:** 1♀ "FRENCH GUIANA: 39 Km Raura, 270m 4º32.72'N 52º08.44'W, 25-29.v.1997 FIT J. Ashe & R. Brooks #76 [CNC493519]"; 1♀ "FRENCH GUIANA: Saul, 7 km S Les Eaux Claires, 170m 31.v-3.vi.1997 R. Brooks FIT" (CNC). **PERU:** ♀ "PERU, CU, La Convención, Echarate, CC. [Comunidad] Kitaparay 72º50'4.31" [W]/12º12'51.79"[S] 608m, 08-11.xi.2009. C. Espinoza y E. Rázuri", 1♀ "Avispas, Peru 30m nr. Marcapata Sept. 1962 Luis Peña" (USUC); 1♀ "PERU: Cusco Dept. [Department], Villa Carmen Fld Stn [Field Station], cafeteria ~1.7 km west research transect, 12.89250ºS 71.41917ºW 555m 21-22.V.2011 DJ Bennett & E Razuri, flight intercept trap, PER-11-FIT-007 [SEMC1037454]" (SEMC); 1♀ "PERU: Madre de Dios, Pantiacolla Lodge, 400m 12º39.3'S 71º13.9'W 23-26.x.2000 R. Brooks FIT" (CNC); 1♀ "PERU: AM. Bagua CCNN. Tutumberis 18-19.iv.2015 5º14'23.4"S/ 78º27'56.2"W 327m L. Sulca", 1♀ "PERU, CU, La Convención, Echarate, CC. [Comunidad] Kitaparay 72º50'4.31" [W]/12º12'51.79"[S] 608m, 08-11.xi.2009. C. Espinoza y E. Rázuri", 1♀ "PERU, CU, La Convención, Echarate, CC. [Comunidad] Kitaparay 72º50'4.31" [W]/12º12'51.79"[S] 608m, 08-11.xi.2009. C.

Espinoza y E. Rázuri”, 1♀ “PERU: CU. La Convención 12º02'42.24S, 72º59'01.91"W 825m, 16.iv.2007, [Malaise] F. Azorsa / Bosque de colinas altas P4-M63”, 4♀♀ “PERU: MD. Manu, Rio Serjali 12º42'55.5"S/ 71º14'31.6"W 428m, 19-21.i.2011 J. Acosta”, 1♂ “PERU: MD, Manu, Rio Blanco 12º43'3.57"S 71º9'19.26"W 466m, 26-28.i.2011, J. Costa”, 1♀ “PERU: MD. Reserva Comunal Amarakaeri 12°58'57.54"S/ 71°1'40.94"W 732m, 30.ix-01.x.2010 Yellow [Pan trap] M. Vilchez, C. Castillo / PM14, A, 10/31, Y4”, 1♀ “PERU: MD. Reserva Comunal Amarakaeri 12º43'16.12"S/ 71º14'22.97"W 428m, 19-21.i.2011 J. Acosta”, 1♀ “PE [PERÚ]: LO [Loreto] Alto Nanay, Albarenga north 128m 18M 0533061E 9645180N 24.xi.2008, C. Castillo / Terrazas bajas inund, [inundables] Flight-intercept 3A MB2”, 1♀ “PE [PERÚ]: LO [Loreto] Alto Nanay, Albarenga north 139m 18M 0530666E 9646496N 20.vii.2008, M. Vilchez / Colinas bajas fuertmnte disect, Malaise trap 4AM2”, 1♀ “PE [PERÚ]: LO [Loreto] Alto Nanay, Albarenga north 157m 18M 0532439E 9646162N 17.xi.2008, C. Castillo / Colinas bajas fuertmnte disect, Malaise trap 17AM2” (metasoma disected and preserved in a vial with glycerine), 1♀ “PE [PERÚ]: LO [Loreto] Río Itaya 18M 0634682E 9528152N 161m, 8.ii.2009, W. Paredes/ Colinas bajas fuertmnte disect, Malaise trap 28T74M2”, 1♀ “PE [PERÚ]: LO [Loreto] Río Itaya 18M 0634682E 9528152N 161m, 8.ii.2009, W. Paredes/ Colinas bajas fuertmnte disect, Malaise trap 28T74M2”, 2♀♀ “PERÚ: UC. Coronel Portillo, Calleria, Abujao 08º19'34.32"S/ 73º39'58.7"W 195m. 23-25.iv.2013 L. Sulca” (metasoma disected and preserved in a vial with glycerine) (MUSM). **SURINAME:** 1♀ “Phedra, Surinam X.13-19.1964 D.C. Geijskes” (USUC).

***Exochus* 7 sp. nov.**

Figures 36, 42

Diagnosis. Face+clypeus 0.8× as long as wide; malar space 1.1–1.2× as long as basal mandibular width; antenna with 34–37 flagellomeres; mesopleuron with epicnemial carina

preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.1–0.3× as long as length of vein Cu1 between M and Cu1; propodeum tawny; metacoxa tawny; metatibia tawny; metasoma dark brown with at least tergite III laterally pale tawny, usually with pale tawny coloration more expanded in the first four tergites.

Description. Female: Forewing length 4.2 mm.

Head. Face+clypeus 0.8× as long as wide (Fig. 42D); malar space 1.2× as long as basal mandibular width; lateral ocellus separated from compound eye by about 1.0× maximum ocellar diameter; distance between ocelli 0.9× maximum ocellar diameter (Fig. 42C); gena in lateral view 0.7× as long as compound eyes; antenna with 37 flagellomeres, ratio of length from second to fourth flagellomeres: 1.1:1.1:1.1, subapical flagellomere elongate, 1.8× as long as centrally broad, clearly longer than broad.

Mesosoma. Mesopleuron (Fig. 42A) with epicnemial carina ending at subalar prominence, preapically interrupted. Submetapleural carina smooth, anteriorly expanded into triangular lobe. Propodeum (Fig. 42B) with anterior and posterior transverse carinae complete; lateromedian longitudinal present between base of propodeum and posterior transverse carina; lateral longitudinal carina present, faint between propodeum basally and anterior transverse carina; area superomedia 1.6× as long as wide. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.5× its own length; Cu1 between 1m-cu and Cu1a 1.7× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.6× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 1.0× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of M sclerotized; length of abscissa of Cu1 between Cu1 and 1A 0.3× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.7× as long as inner spur.

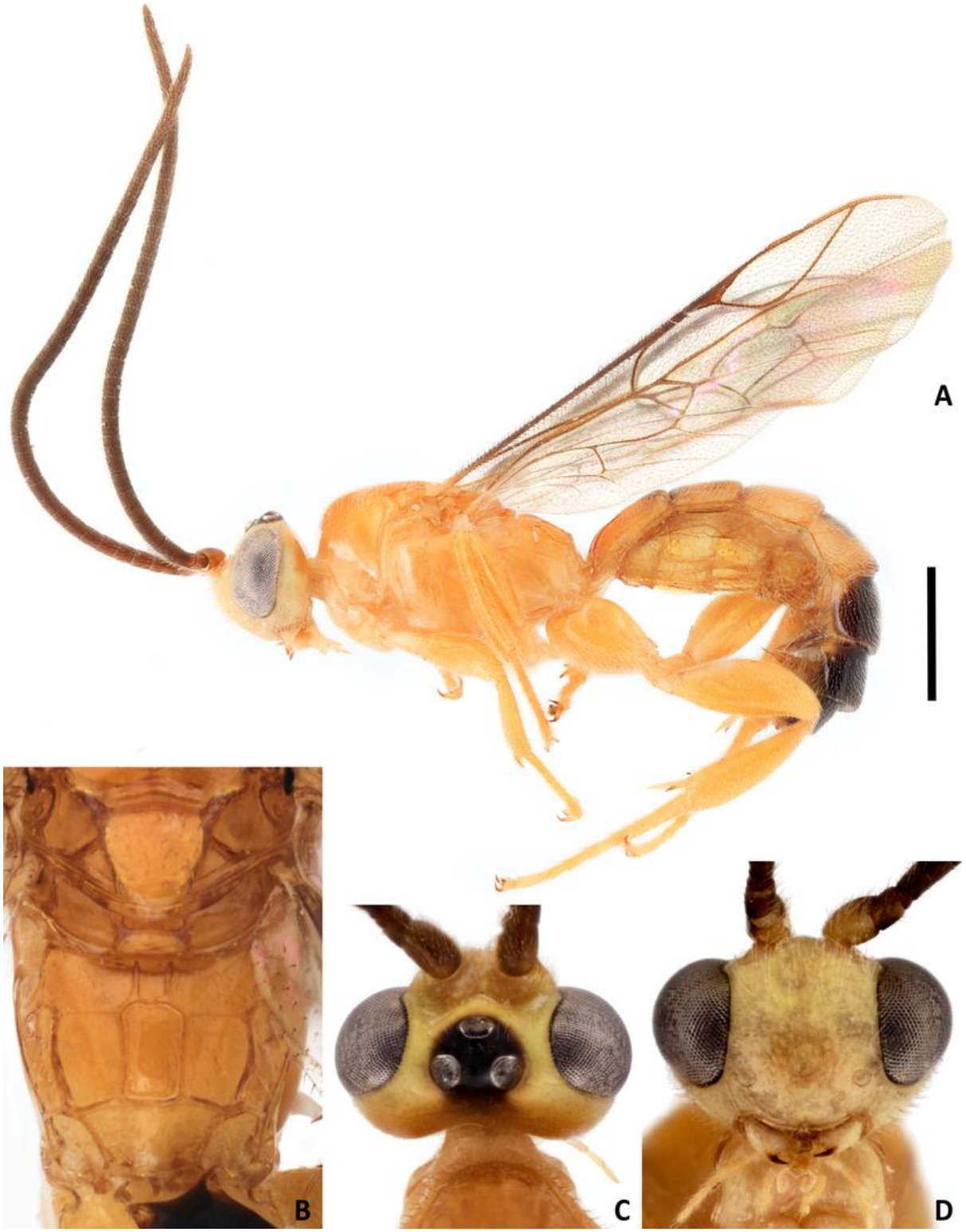

Figure 42. Morphology of *Exochus* 7 sp. nov., female. **A.** Lateral habitus (scale bar=1mm). **B.** Dorsal view of propodeum. **C.** Dorsal view of head. **D.** Head, facial view.

Metasoma. Tergite I 1.1× as long as posteriorly wide, lateromedian carinae extending 0.6× length of tergite; tergite II 0.7× as long as posteriorly wide; laterotergite II 0.2× as long as wide; laterotergite III 0.4× as long as wide, semicircular, mesal edge convex.

Color. Head (Figs. 42C, 42D) mostly pale yellow with interocellar area black, occiput centrally brownish; antenna dark brown, scape and pedicel ventrally yellowish. Mesosoma tawny (Fig. 42A). Metasoma dark brown; tergite I predominantly pale tawny distally brownish; tergite II and III predominantly pale tawny, basally brownish; tergite IV pale tawny, centrally brownish.

Variation. The female paratypes differ from the holotype in the following: Forewing length 3.7–4.9 mm; malar space 1.1–1.2× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.8–0.9× maximum ocellar diameter; distance between ocelli 0.7–0.9× maximum ocellar diameter; gena in lateral view 0.6–0.8× as long as compound eyes; antenna with 34–37 flagellomeres, ratio of length from second to fourth flagellomeres: 1.1–1.3:1.1–1.2:1.1–1.2, subapical flagellomere elongate, 1.4–1.8x as long as centrally broad; propodeum with area superomedia 1.6–1.8× as long as wide; forewing with crossvein 1cu-a distal to base of Rs&M about 0.5–0.6× its own length, Cu1 between 1m-cu and Cu1a 1.6–2.1× as long as Cu1b, Cu1a between Cu1b and 2m-cu 1.3–1.6× as long as Cu1 between Rs&M and 1m-cu, 2rs-m 0.8–1.1× as long as abscissa of M between 2rs-m and 2m-cu; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.1–0.3× as long as length of vein Cu1 between M and Cu1; tergite I 1.1–1.2× as long as posteriorly wide, lateromedian carinae extending 0.5–0.6× length of tergite; laterotergite III 0.4–0.5× as long as wide.

There is considerable variation in the coloration of the species especially in the coloration of the metasomal tergites, all individuals with at least tergite III laterally pale tawny; usually with pale tawny coloration more expanded on the first four tergites. Head in some individuals with a continuous black mark from interocellar area to occiput centrally or occiput not marked by black.

Male: Unknown.

Distribution. This species (Fig. 36) was collected Brazil, Ecuador, French Guiana, and Peru, in wet forest between sea level to 815 m.

Remarks. This species was collected using Malaise traps, yellow pan traps, and FITs. It is the first record of the genus for Ecuador and French Guiana.

Examined material. BRAZIL: 1♀ "Vihena, Rond. XI.'73 Brazil M. Alvarenga" (USUC). **ECUADOR:** 1♀ "Ecuador: Napo Misahualli Feb. 19, 1983 L. Huggert", 1♀ "ECUADOR: Pastaza, Kapawi, 2.55ºS, 76.82ºW, 300m; 6-20.iii.1996; P. Hibbs; Malaise trap" (USUC). **FRENCH GUIANA:** 3♀♀ "FRENCH GUIANA: Patawa, Kaw Mountain, 4º33.562'N 52º12.425'W 12.ii-3.iii.2007 Malaise trap, K. Sarv", 1♀ "FRENCH GUIANA: PK35 4º32.663'N 52º09.371'W 230m 5.xii.2007, Malaise trap, rain forest, J. Cerda" (CNC). **PERU:** 1♀ "PERU: MD. Reserva Comunal Amarakaeri, 70º45'35.64"W/ 13º3'25.78"S 333m, 09.xi.2010 [Malaise] M. Vilchez y C. Castillo / PM16, B, 11/08, M3", 1♀ "PERÚ: CU, Reserva Comunal Amarakaeri, 29.ix.2010 m, 12º55'25.9"S/ 70º4'9.6W 503m Malaise, C. Castillo / PM3, , 09/29 M1" 1♀ "PERU: CU, San Martin-3 Camp, 3.xi.1997, 474m, 11º47'S/72º42'W, Malaise trap, Camisea project / SM01.1103 M05" (hind legs missing), 2♀♀ "PERÚ: CU. Valle del Qosñipata, Tono. 12º57'21.6"S/ 71º33'13.9"W 26.ix.2007 815m. [Malaise trap] C. Castillo Leg." (MUSM); 3♀♀ "Avispas, Peru 30m nr. Marcapata Oct. 1-15, 1962 Luis Peña", 1♀ "PERU: Huanuco, Tingo Maria; 27 Jan. 1984; L. Huggert" (USUC); 1♀ "PE[PERU] Lo, Rio Copalyacu, 3º46'39"S/ 75º25'31"W 119m, malaise trap. 10.xii.2009, L. Sulca", 1♀ "PERU: MD. Manu, Rio Serjali 12º42'55.5"S/ 71º14'31.6"W 428m, 19-21.i.2011 J. Acosta" (molecular extractions done), 1♀ "PERU: MD. Reserva Comunal Amarakaeri, Rio Azul 71º05'55.11"W/ 12º49'7.75"S 507m, 12.x.2011 M. Vilchez y C. Castillo" 1♀ "PERU: MD. Reserva Comunal Amarakaeri, Rio Dahuene 12º50'16.26"S/ 70º52'17.1"W 365m, 31.v-02.vi.2011 Malaise, B. Medina y L. Huerto" (right leg missing), 1♀ "PERU: MD, Reserva Comunal Amarakaeri, 333m 12º56'32.48"S/ 70º48'23.30"W 24-

26.x.2010, M. Vílchez/ PM8, A, 10/26 Y4" molecular extractions done), 1♀ "PERÚ: UC. Coronel Portillo, Calleria 73º42'35.1"W/ 08º26'9.77"S 227m. 17.x.2012 B. Medina" (molecular extractions done) (MUSM).

***Exochus* 8 sp. nov.**

Figures 43, 44

Diagnosis. Face+clypeus 0.8× as long as wide; malar space 1.2× as long as basal mandibular width; antenna with 34–36 flagellomeres; mesopleuron with epicnemial carina preapically interrupted; propodeum with transverse and longitudinal carinae well defined, area superomedia and dentipara enclosed; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.2–0.3× as long as length of vein Cu1 between M and Cu1; propodeum tawny; metacoxa tawny; metatibia tawny; metasomal tergites dark brown with at least tergite III laterally tawny.

Description. Female: Forewing length 4.6 mm.

Head. Face+clypeus 0.8× as long as wide (Fig. 43C); malar space 1.2× as long as basal mandibular width; lateral ocellus separated from compound eye by about 0.9× maximum ocellar diameter; distance between ocelli 0.6× maximum ocellar diameter (Fig. 43D); gena in lateral view 0.5× as long as compound eyes; antenna with 35 flagellomeres, ratio of length from second to fourth flagellomeres: 1.1:1.1:1.0, subapical flagellomere elongate, 1.3× as long as centrally broad.

Mesosoma. Mesopleuron with epicnemial carina ending at subalar prominence, preapically interrupted. Submetapleural carina smooth, anteriorly expanded into conspicuous semicircular lobe. Propodeum (Fig. 43B) with anterior and posterior transverse carinae complete; lateromedian longitudinal present between base of propodeum and posterior transverse carina; lateral longitudinal carina present, absent between propodeum basally and

anterior transverse carina; area superomedia 1.6× as long as wide. Forewing with crossvein 1cu-a distal to base of Rs&M about 0.4× its own length; Cu1 between 1m-cu and Cu1a 2.8× as long as Cu1b; Cu1a between Cu1b and 2m-cu 1.7× as long as Cu1 between Rs&M and 1m-cu; 2rs-m 1.0× as long as abscissa of M between 2rs-m and 2m-cu. Hind wing with distal abscissa of M sclerotized; length of abscissa of Cu1 between Cu1 and 1A 0.2× as long as length of vein Cu1 between M and Cu1. Outer metatibial spur 0.6× as long as inner spur.

Metasoma. Tergite I 1.4× as long as posteriorly wide, lateromedian carinae extending 0.5× length of tergite (Fig. 43B); tergite II 0.8× as long as posteriorly wide; laterotergite II 0.1× as long as wide; laterotergite III 0.4× as long as wide, semicircular, mesal edge convex.

Color. Head (Figs. 43C, 43D) mostly pale yellow with interocellar area black, occiput centrally brownish; antenna dark brown, scape ventrally yellowish. Mesosoma tawny. Metasoma (Fig. 43A, 43B) dark brown; tergite I tawny, basally and distally brownish; tergite II tawny, distally brownish; tergite III laterally tawny.

Variation. The female paratypes differ from the holotype in the following: forewing length 4.0–4.6 mm; lateral ocellus separated from compound eye by about 0.8–0.9× maximum ocellar diameter; antenna with 34–36 flagellomeres, ratio of length from second to fourth flagellomeres: 1.1:1.1:1.0–1.1, subapical flagellomere elongate, 1.3–1.6× as long as centrally broad; forewing with crossvein 1cu-a distal to base of Rs&M about 0.4–0.5× its own length, Cu1 between 1m-cu and Cu1a 2.4–3.0× as long as Cu1b, Cu1a between Cu1b and 2m-cu 1.3–1.7× as long as Cu1 between Rs&M and 1m-cu, 2rs-m 0.7–1.3× as long as abscissa of M between 2rs-m and 2m-cu; hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.2–0.3× as long as length of vein Cu1 between M and Cu1; outer metatibial spur 0.6–0.7× as long as inner spur; tergite I 1.4–1.5× as long as posteriorly wide, lateromedian carinae extending 0.5–0.6× length of tergite; laterotergite III 0.4–0.5× as long as wide. Within this species there is some variation especially in the coloration of the metasomal tergites. All

individuals have at least tergite III laterally tawny, and tergites I and II evenly tawny or dark brown, while the occiput is brown centrally.

Figure 43. Morphology of *Exochus* 8 sp. nov., female. **A.** Lateral habitus (scale bar=1mm) **B.** Dorsal view of propodeum and first three metasomal tergites. **C.** Head, frontal view. **D.** Dorsal view of head.

Male: Unknown.

Distribution. This species (Fig. 44) was collected in primary rain forest between 1,593–2,170 m; one individual was collected in a *Podocarpus* forest.

Remarks. This species was collected using only light traps.

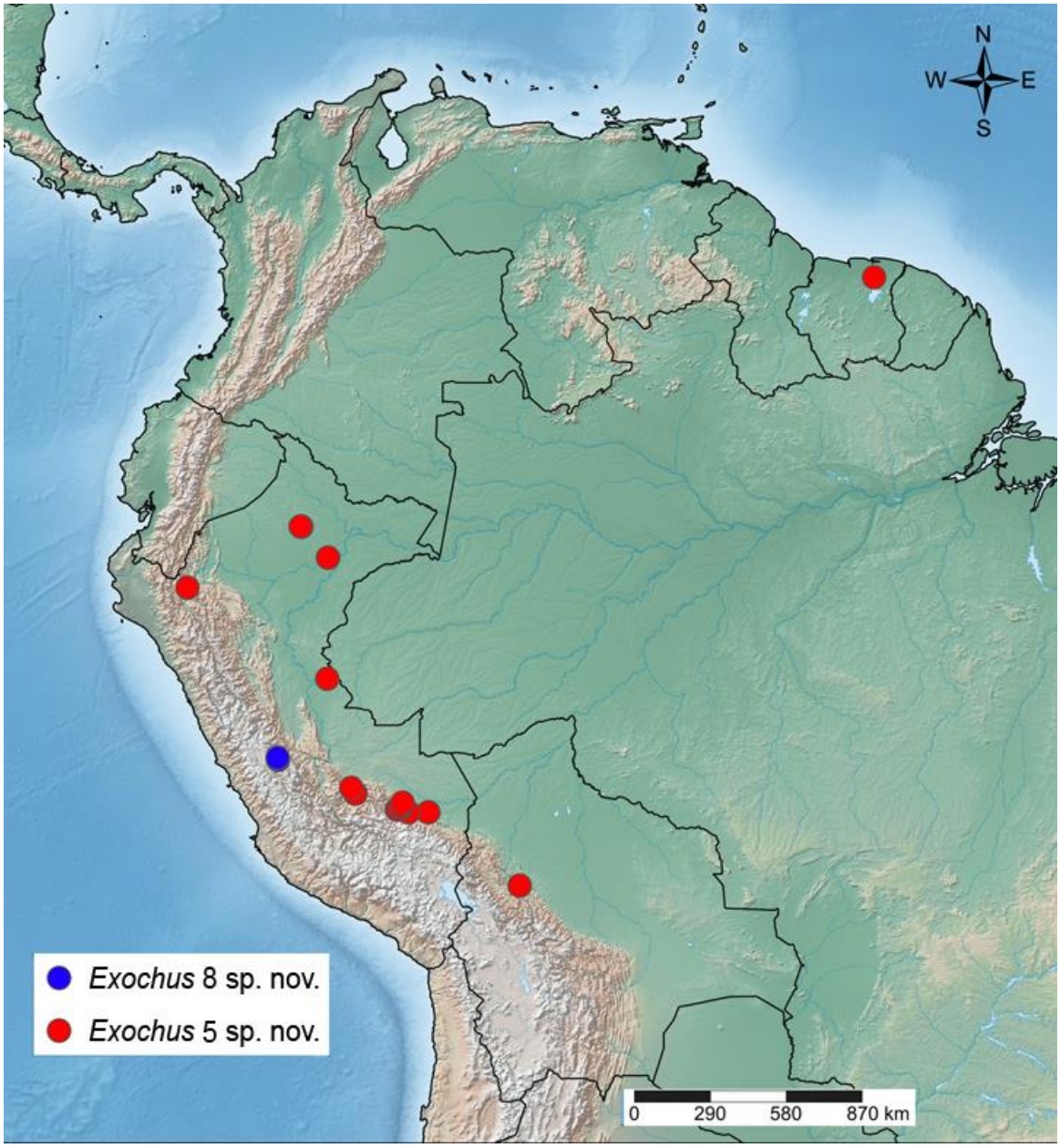

Figure 44. Localities of *Exochus* 5 sp. nov. and *Exochus* 8 sp. nov.

Examined material. PERU: 1♀ "PERU: JU, Chanchamayo, SN [Santuario Nacional] Pampa Hermosa, 10º59'51.8"S/75º25'35.9"W, 1940 m. *Podocarpus* forest 23-31.v.201[2011]. Light trap. M. Alvarado leg. / DNA Ichn 000200" (MUSM), left leg removed, 1♀ "PERU: JU, Chanchamayo, Cerro Pichita APRODES Station, W of San

Ramon, 11°05'39.4"S/ 75°25'31.1"W, 2170m. 05.xi.2009 C. Carrera", 1♀ "PERU: JU, Chanchamayo, SN[Santuario Nacional] Pampa Hermosa, 10º59'48.9"S/75º25'35.3"W, 1593m. 23-31.v.201[2011]. Light trap. M. Alvarado leg. / DNA Ichn 000142", left leg removed; and ♀ "PERU: JU, Chanchamayo, SN[Santuario Nacional] Pampa Hermosa, 10º59'48.9"S/75º25'35.3"W, 1593m. 23-31.v.201[2011]. Light trap. M. Alvarado leg. / DNA Ichn 000141", left leg removed and metasoma missing (MUSM).

Key to the *Exochus albiceps* species-group

1. Antenna with 26–27 flagellomeres; female with malar space 0.8–0.9× as long as basal mandibular width …… ***tegularis* Asmead**

—. Antenna with 33–40 flagellomeres; female with malar space 1.1–1.7× as long as basal mandibular width ……..… 2

2. Propodeum with posterior transverse carina faint or absent between lateral longitudinal carinae (Fig. 35B) …… ***Exochus* 1 sp. nov.**

—. Propodeum with posterior transverse carina present between lateral longitudinal carinae (like, Fig. 30D) ……..… 3

3. Hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.5–0.9× as long as length of vein Cu1 between M and Cu1(like, Fig. 27A); metatibia brown ……... 4

—. Hind wing with length of abscissa of Cu1 between Cu1 and 1A 0.1–0.3× as long as length of vein Cu1 between M and Cu1 (like, Fig. 30A); metatibia off white or pale yellow, dorsally brownish (like, Fig. 30A) ……..… 8

4. Metafemur yellowish tawny with (Fig. 27A) or without (Fig. 35A) a brownish spot distally ……... 5

—. Metafemur predominately brownish black (Figs. 32A, 40A) ……..… 7

5. Frons and occiput tawny (Fig. 37C); metasoma brownish red (Fig. 37A) … ***Exochus* 2 sp. nov.**

—. Frons and occiput black (Figs. 27C, 40B); metasoma brownish black (Figs. 27A, 40A) …… 6

6. Malar space 1.5× as long as basal mandibular width; pro- and mesofemura entirely pale tawny (Fig. 41A) ……..…… ***Exochus* 5 sp. nov. (male)**

—. Malar space 1.1× as long as basal mandibular width; pro- and mesofemura brownish with pale tawny coloration near joints (Fig. 27A) ……..…… ***ablatus* Gauld & Sithole**

7. Metacoxa (Fig. 32A) and propodeum predominantly black (Fig. 32B) ... ***jacintus* Gauld & Sithole**

—. Metacoxa (Fig. 40A) and propodeum (Fig. 40D) predominantly orange … ***Exochus* 5 sp. nov. (female)**

8. Metasoma with tergites III–V entirely tawny (Fig. 28A) …….. ***albiceps* Walsh (female)**

—. Metasoma with tergites III–V entirely black (Figs. 38A, 39A) or black but laterally yellowish white (Fig. 30A), testaceous or tawny (Fig. 43B); or if some tergites tawny, then tergite V black or blackish brown (Fig. 42A) ……...… 9

9. Metacoxa, metafemur and metatibia whitish cream with blackish stripes (like, Fig. 30A) ……..… 10

—. Metacoxa, metafemur, and metatibia yellowish tawny (Figs. 38A, 42A, 43A) ……..… 12

10. Metasoma entirely black (Fig. 39A); metacoxa off white with a ventral longitudinal black mark (Fig. 39A); tergite II 0.8× as long as posteriorly wide … ***Exochus* 4 sp. nov. (male)**

—. Metasoma black with laterally off white at least in tergite III; metacoxa off white with an external lateral longitudinal black mark (like, Figs. 30A or 33A); tergite II 0.6–0.7× as long as posteriorly wide …….. 11

11. Metasoma black with lateral and distal margins of tergites III–VII off yellow; Nearctic region …….. ***albiceps* Walsh (male)**

—. Metasoma black with lateral margin tergites of III–VII off white; Neotropical region ……..… ***izbus*** **Gauld & Sithole**

12. Metasoma entirely black (Fig. 38A) ……..… ***Exochus*** **4 sp. nov. (female)**

—. Metasoma black with tawny spots in at least on tergum III (Fig. 43B) …… 13

13. Metasoma with tergite I 1.1–1.2× as long as posteriorly wide …… ***Exochus*** **7 sp. nov.**

—. Metasoma with tergite I 1.4–1.5× as long as posteriorly wide …… ***Exochus*** **8 sp. nov.**

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APPENDICES

Appendix 4. List of the species used in the phylogenetic analysis. EM = External morphology.

TAXA	GEOGRAPHIC DISTRIBUTION	COLLECTION	♀	♂	EM	♂ genitalia
OUTGROUP						
Exochus sp. 12	Peru	MUSM	x	x	x	x
Exochus sp. 63	Peru	MUSM	x		x	
Exochus sp. Uruguay	Uruguay	INPA	x	x	x	x
INGROUP						
Exochus ablatus Gauld & Sithole, 2002	Costa Rica, Panama	USUC	x		x	
Exochus albiceps Walsh, 1873	United States	USUC	x		x	
Exochus izbus Gauld & Sithole, 2002	Argentina, Bolivia, Costa Rica, Ecuador, French Guiana, Guatemala, Honduras, Mexico, Panama, Peru, Uruguay, and Venezuela.	CNC, MUSM, SEMC, USUC	x	x	x	x
Exochus jacintus Gauld & Sithole, 2002	Brazil, Costa Rica, French Guiana, Paraguay, Peru, Trinidad and Tobago, and Venezuela	CNC, MUSM, SEMC, USUC	x		x	
Exochus tegularis Ashmead, 1894	Martinique, Saint Lucia	CNC	x	x	x	x
Exochus 1 sp. nov.	Peru	MUSM	x	x	x	x
Exochus 2 sp. nov.	Brazil	USUC	x		x	
Exochus 4 sp. nov.	Peru	MUSM, SEMC	x	x	x	x
Exochus 5 sp. nov.	Bolivia, French Guiana, Peru, Suriname	MUSM, USUC	x	x	x	x
Exochus 7 sp. nov.	Brazil, Ecuador, French Guiana, Peru	CNC, MUSM, USUC	x		x	
Exochus 8 sp. nov.	Peru	MUSM	x		x	

Appendix 5. List of specimens studied for molecular extractions of mitochondrial NADH dehydrogenase 1 (ND1), and nuclear 28S rRNA (28S) and wingless (Wg), gene regions amplified, depository institution and collecting data.

TAXA	28S	NAD	Wg	Depository	Data
OUTGROUP					
*Exochus*_12	x	x	x	MUSM	PERÚ: LI. Sánchez Carrión, Huamachuco, 7°55'39.41"S/ 78° 8'55.28"O, 3670m, 29.iv.2015, E. Gamboa
*Exochus*_Uruguay	x		x	INPA	URUGUAY: Rocha, Don Bosco, 34º05'02.6"S/ 53º45'44.5"O, 26.ii.2015, Malaise 2, bosque-campo, E. Castiglioni e eq., cols.

*Exochus*_63_Ich98	x	x	x	MUSM	PERÚ: JU. Chanchamayo, SN [Santuario Nacional] Pampa Hermosa 10º59'48.9"S/ 75º25'35.3"W 1593m. 23-31.v.2011. Light trap. M. Alvarado
*Exochus*_63_Ich115	x	x		MUSM	PERÚ: JU. Chanchamayo, SN [Santuario Nacional] Pampa Hermosa 10º59'48.9"S/ 75º25'35.3"W 1593m. 23-31.v.2011. Light trap. M. Alvarado
*Exochus*_63_Ich140	x	x		MUSM	PERÚ: JU. Chanchamayo, SN [Santuario Nacional] Pampa Hermosa 10º59'48.9"S/ 75º25'35.3"W 1593m. 23-31.v.2011. Light trap. M. Alvarado
INGROUP					
Exochus izbus					
*Exochus_izbus*_1	x			MUSM	PERU: AM, Bagua CCNN. Tutumberos 5º20'2.9"S, 78º27'12.5"W, 366m, 17-18.iv.2015 L. Sulca
*Exochus_izbus*_Guatemala	x			SEMC	GUATEMALA: Suchitepequez; Volcan Atitlan, Ref. El Quetzal 1660m 14.55012 -91.19377 14-18-XI-2016 ZHFalin & FCarillo ex. Flight intercept trap, wet montane forest GUAT1F16 016.
*Exochus_izbus*_CR	x			SEMC	COSTA RICA: Puntarenas Prov. Altamira Biol. Sta., 1510-1600m 09º01.76'N, 83º00.49'W 4-7-VI-2004, J.S. Ashe, Z. Falin, I. Hinojosa, Ex: fligth intercept trap. CR1AFH04 144
*Exochus_izbus*_PERU_MD	x			MUSM	PERU: MD, Reserva Comunal Amarakaeri, 70o57'56.9"W/ 13o5'45.68"S 578m, 21-22.v.2011 Malaise B. Medina y L. Huerto
*Exochus_izbus*_Venezuela	x			CNC	VENEZUELA: Aragua, Rancho Grande Biological Station, 1140m, 1-6.iii.1995 FIT R. Brooks / CNC493267
*Exochus_izbus*_FG	x			CNC	FRENCH GUIANA: Patawa, Kaw Mountain, viii.2008, Malaise trap, J. Cerda / CNC 493512
*Exochus_izbus*_URUGUAY	x			INPA	URUGUAY: Rocha, Don Bosco, 34º05'02.6"S/ 53º45'44.5"O, 26.ii.2015, Malaise 2, bosque-campo, E. Castiglioni e eq., cols.
*Exochus_izbus*_PERU_JU	x		x	MUSM	PERÚ: JU. Chanchamayo, Pichanaqui, San Miguel de Autiki, 10º48'16.59"S/ 74º49'33.40"W, 1464m, 02-07.vi.2014 E. Rázuri
*Exochus_izbus*_2	x			MUSM	PERU: CU, La Convención, Echarate, Comunidad Nueva Luz, 73º01'13" [W]/ 11o39'15.6"[S] 407m. 16.vii.2013 V. Borda
Exochus jacintus					
*Exochus_jacintus*_3	x			MUSM	PERU: MD. Tambopata, Explorer's Inn, 12º50'44.2"S/ 69º17'34.5"W 189m. 23.ii.2010, M. Alvarado
*Exochus_jacintus*_FG	x			CNC	FRENCH GUIANA: 18.4 Km SSE Roura, 240m 29.v-10.vi.1997 J. Ashe & R. Brooks FIT#180 / CNC493278

*Exochus_jacintus*_PERU_JU	x	x		MUSM	PERÚ: JU. Chanchamayo, Pichanaqui, San Miguel de Autiki, 10º48’16.59”S/ 74º49’33.40”W, 1464m, 02-07.vi.2014 E. Rázuri
Exochus tegularis					
*Exochus_tegularis_* Martinique	x			MUSM	MARTINIQUE: 2 Km NW Diamant 14º29.4’N 61º02.5’W 6-23.vii.2010 Thorn forest 80m Malaise trap J. Peck / CNC493243
*Exochus_tegularis*_Saint_ Lucia	x	x		MUSM	SAINT LUCIA: West Indies 14-21.v.1971, Univ. of Waterloo
Exochus 1 sp. nov.					
*Exochus*_1_5	x			MUSM	PERU: AM. Bagua CCNN. Tutumberos 18-19.iv.2015 5º14'23.4"S/ 78º27'56.2"W 327m L. Sulca
*Exochus*_1_1_PERU_CY	x			MUSM	PERU: CU. La Convención, Echarate, CC. Santa Rosa 12º33'55.00"S/ 73º05'37.35"W 1482m, 18-21.ix.2010. MA[Malaise] M. Alvarado y J. Peralta
*Exochus*_1_2_PERU_PA	x			MUSM	PERÚ: PA. Villa Rica, ZA del Bosque de Protección San Matias San Carlos 75º12'37"/10º38'44" 1596m. 6-10.viii.2012 Malaise trap P. Sanchez & E. Razuri
Exochus 4 sp. nov.					
*Exochus*_4_8	x			MUSM	PERU: CU, Paucartambo, Kosñipata, Wayqecha, intersection Trocha Oso with Trocha Mariposa, 2533 m, 13º09’57.9”S, 71º35’22.3”W, 31.x.2017, cloud forest, FIT, M. Rodríguez & L. Pérez leg.
*Exochus*_4_25_PERU_CU	x			MUSM	PERÚ: CU. Qosñipata Valley, San Pedro. 13º2'59"S/ 71º32'13"W 1500m. 23.vii.2007 Malaise trap 1500 C. Castillo
*Exochus*_4.44_PERU_CY	x			MUSM	PERU, CU, La Convención, Echarate, CC. [Comunidad] Santa Rosa 12º33'55.00" [S] /73º05'37.35" [W] 1482m, 18-21.ix.2010. MA M. Alvarado y J. Peralta
*Exochus*_4.5_PERU_CU	x			MUSM	PERÚ: CU, C.I. [Centro de Investigacion] Wayquecha 13º10'31"S/ 71º34'53"W 11.ix.2007. 2692m, Malaise trap 5 C. Castillo leg
*Exochus*_4.6_PERU_CU	x			MUSM	PERÚ: CU, C.I. [Centro de Investigacion] Wayquecha 13º10'31"S/ 71º34'53"W 11.ix.2007. 2692m, Malaise trap 5 C. Castillo leg
*Exochus*_4.26_PERU_PA	x			MUSM	PERÚ: PA. Villa Rica, ZA del Bosque de Protección San Matias San Carlos 75º12'37"/10º38'44" 1596m. 6-10.viii.2012 Malaise trap P. Sanchez & E. Razuri
Exochus 5 sp. nov.					
*Exochus*_5_4	x			MUSM	PERÚ: JU. SN [Santuario Nacional] Pampa Hermosa 10º59'52.7"S/ 75º25'34.3"W 1757m. 30.v.2011 D. Silva

					leg
*Exochus*_5_2_PERU_MD	x			MUSM	PERU: MD. Reserva Comunal Amarakaeri 12º43'16.12"S/ 71º14'22.97"W 428m, 19-21.i.2011 J. Acosta
*Exochus*_5.1_PERU_UC	x			MUSM	PERÚ: UC. Coronel Portillo, Calleria, Abujao 08º19'34.32"S/ 73º39'58.7"W 195m. 23-25.iv.2013 L. Sulca
*Exochus*_5_3_French_Guyana	x			CNC	FRENCH GUIANA: 39 Km Raura, 270m 4º32.72'N 52º08.44'W, 25-29.v.1997 FIT J. Ashe & R. Brooks #76 / CNC493519
Exochus 7 sp. nov.					
*Exochus*_7.1_PERU_MD	x			MUSM	PERU: MD. Manu, Rio Serjali 12º42'55.5"S/ 71º14'31.6"W 428m, 19-21.i.2011 J.Acosta
*Exochus*_7.2_PERU_UC	x			MUSM	PERÚ: UC. Coronel Portillo, Calleria, Abujao 08º19'34.32"S/ 73º39'58.7"W 195m. 23-25.iv.2013 L. Sulca
Exochus 8 sp. nov.					
*Exochus*_8_Ich141	x	x	x	MUSM	PERU: JU, Chanchamayo, SN Pampa Hermosa, 10º59'48.9"S/ 75º25'35.3"W, 1593m. 23-31.v.201[2011]. Ligth trap. M. Alvarado leg.
Exochus_8_Ich142	x	x	x	MUSM	PERU: JU, Chanchamayo, SN Pampa Hermosa, 10º59'48.9"S/ 75º25'35.3"W, 1593m. 23-31.v.201[2011]. Ligth trap. M. Alvarado leg.
Exochus_8_Ich200	x		x	MUSM	PERU: JU, Chanchamayo, SN Pampa Hermosa, 10º59'51.8"S/75º25'35.3"W, 1940 m. Podocarpus forest 23-31.v.201[2011]. Ligth trap. M. Alvarado leg.

Appendix 6. Character matrix used in the phylogenetic analyses of *Exochus*. Dash (–) = not applicable; question marks (?) were used when the characters could not be codified.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Exochus 12	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Exochus Uruguay	1	0	0	0	1	0	0	0	1	0	0	0	0	1
Exochus 63	1	0	1	1	0	1	0	0	1	1	0	1	?	?
Exochus ablatus	0	1	1	1	1	1	1	1	0	1	0	1	?	?
Exochus 1 sp. nov.	0	1	1	1	1	1	1	1	1	0	0	1	1	0
Exochus albiceps	0	1	1	1	1	1	0	1	0	1	0	1	?	?
Exochus 7 sp. nov.	0	1	1	1	1	1	0	1	0	0	1	1	?	?
Exochus izbus	0	1	1	0	1	1	0	1	0	1	1	1	2	0
Exochus jacintus	0	1	1	1	1	1	1	1	0	1	0	1	?	?
Exochus 2 sp. nov.	0	1	1	1	1	1	1	1	0	1	0	1	?	?
Exochus 8 sp. nov.	0	1	1	1	1	1	0	1	0	0	1	1	?	?
Exochus tegularis	0	1	1	0	1	1	0	1	0	1	1	0	2	0
Exochus 5sp. nov.	0	1	1	1	1	1	1	1	0	1	0	1	1	0
Exochus 4 sp. nov.	0	1	1	1	1	1	0	1	0	0	0	1	1	0

Appendix 7. Primer sequences and PCR protocols used in this study.

Marker	Primer name	Source	Sequence	Annealing, extension temperature (˚C)
28S	For28Vesp	Hines *et al*. 2007	AGAGAGAGTTCAAGAGTACGTG	49, 60
	Rev28Vesp	Hines *et al*. 2007	GGAACCAGCTACTAGATGG	
Wg	Wg587F	Ward & Downie (2005)	TGCACNGTGAARACYTGCTGGATG	54, 72
	WgAbR	Abouheif & Wray (2002)	ACYTCGCAGCACCARTGGAA	
ND1	ND1F	Klopfstein *et al*. 2011	ACTAATTCAGATTCTCCTTCTG	46, 68
	ND1R	Klopfstein *et al*. 2011	CAACCTTTTAGTGATGCTATTAA	

Appendix 8. Matrix of genetic distances for NADH dehydrogenase 1 sequences. Numbers indicate genetic similarity as a percentage of shared bases among respective taxa; i.e lower values indicate greater genetic distances.

	*Exochus*_12	Exochus_63_Ich98	Exochus_63_Ich115	Exochus_63_Ich140	Exochus_jacintus_PERU_JU	Exochus_tegularis_Saint_Lucia	Exochus_8_Ich141	Exochus_8_Ich142
*Exochus*_12		72.14	71.74	72.14	85.57	78.36	78.61	78.1
*Exochus*_63_Ich98	72.14		100	100	74.13	73.88	70.4	69.75
*Exochus*_63_Ich115	71.74	100		100	74.18	74.46	71.2	70.5
*Exochus*_63_Ich140	72.14	100	100		74.13	73.88	70.4	69.75
*Exochus_jacintus*_PERU_JU	85.57	74.13	74.18	74.13		79.85	80.1	79.11
*Exochus_tegularis*_Saint_Lucia	78.36	73.88	74.46	73.88	79.85		82.59	82.15
*Exochus*_8_Ich141	78.61	70.4	71.2	70.4	80.1	82.59		99.11
*Exochus*_8_Ich142	78.1	69.75	70.5	69.75	79.11	82.15	99.11	

Appendix 9. Matrix of genetic distances for nuclear 28S rRNA sequences. Numbers indicate genetic similarity as a percentage of shared bases among respective taxa; i.e lower values indicate greater genetic distances.

	*Exochus*_12	*Exochus*_Uruguay	*Exochus*_63_Ich98	*Exochus*_63_Ich115	*Exochus*_63_Ich140	*Exochus_izbus*_1	*Exochus_izbus*_Guatemala	*Exochus_izbus*_CR	*Exochus_izbus*_PERU_MD
*Exochus*_12		98.55	95.73	95.73	95.74	95.77	95.75	95.69	95.69
*Exochus*_Uruguay	98.55		95.87	95.87	95.87	96.42	96.52	96.49	96.49
*Exochus*_63_Ich98	95.73	95.87		100	100	94.84	95	94.94	94.94
*Exochus*_63_Ich115	95.73	95.87	100		100	94.84	95	94.94	94.94
*Exochus*_63_Ich140	95.74	95.87	100	100		94.84	95.02	94.94	94.94
*Exochus_izbus*_1	95.77	96.42	94.84	94.84	94.84		100	100	100
*Exochus_izbus*_Guatemala	95.75	96.52	95	95	95.02	100		100	100
*Exochus_izbus*_CR	95.69	96.49	94.94	94.94	94.94	100	100		100
*Exochus_izbus*_PERU_MD	95.69	96.49	94.94	94.94	94.94	100	100	100	
*Exochus_izbus*_Venezuela	95.69	96.49	94.94	94.94	94.94	100	100	100	100
*Exochus_izbus*_FG	95.75	96.52	95	95	95.02	100	100	100	100
*Exochus_izbus*_URUGUAY	95.75	96.52	95	95	95.02	100	100	100	100
*Exochus_izbus*_PERU_JU	95.75	96.36	94.84	94.84	94.86	100	99.84	99.84	99.84
*Exochus_izbus*_2	94.46	95.11	93.55	93.55	93.55	98.7	98.7	98.7	98.7
*Exochus_jacintus*_3	93.91	95.28	93.17	93.17	93.19	96.77	96.88	96.84	96.84
*Exochus_jacintus*_FG	93.91	95.28	93.17	93.17	93.19	96.77	96.88	96.84	96.84
*Exochus_jacintus*_PERU_JU	93.28	94.5	92.39	92.39	92.41	96.13	96.11	96.04	96.04
*Exochus_tegularis*_Martinique	95.44	96.2	94.69	94.69	94.7	99.67	99.69	99.68	99.68
*Exochus_tegularis*_Saint_Lucia	95.75	96.52	95	95	95.02	100	100	100	100
*Exochus*_1_5	95.75	97.15	95	95	95.02	99.02	99.06	99.04	99.04
*Exochus*_1_1_PERU_CY	95.66	97.11	94.9	94.9	94.9	99.02	99.04	99.04	99.04
*Exochus*_1_2_PERU_PA	95.74	97.15	95	95	95	99.02	99.05	99.04	99.04
*Exochus*_5_4	95.13	96.52	94.38	94.38	94.39	98.37	98.43	98.4	98.4
*Exochus*_5_2_PERU_MD	95.13	96.52	94.38	94.38	94.39	98.37	98.43	98.4	98.4
*Exochus*_5.1_PERU_UC	95.11	96.52	94.38	94.38	94.38	98.37	98.42	98.4	98.4
*Exochus*_5_3_French_Guyana	95.43	96.84	94.69	94.69	94.69	98.7	98.74	98.72	98.72
*Exochus*_4_8	95.74	96.03	94.2	94.2	94.22	98.05	97.96	97.92	97.92
*Exochus*_4_25_PERU_CU	95.65	96.13	94.25	94.25	94.25	98.05	98.07	98.07	98.07
*Exochus*_4.44_PERU_CY	95.65	96.13	94.25	94.25	94.25	98.05	98.07	98.07	98.07
*Exochus*_4.5_PERU_CU	95.67	96.15	94.29	94.29	94.29	98.05	98.08	98.08	98.08
*Exochus*_4.6_PERU_CU	95.67	96.15	94.29	94.29	94.29	98.05	98.08	98.08	98.08
*Exochus*_4.26_PERU_PA	95.74	96.19	94.36	94.36	94.38	98.05	98.11	98.08	98.08
*Exochus*_7.1_PERU_MD	95.73	96.19	94.36	94.36	94.36	98.05	98.11	98.08	98.08
*Exochus*_7.2_PERU_UC	95.11	96.19	94.36	94.36	94.38	98.05	98.11	98.08	98.08
*Exochus*_8_Ich141	95.74	96.19	94.36	94.36	94.38	98.05	98.11	98.08	98.08
*Exochus*_8_Ich142	95.74	96.19	94.36	94.36	94.38	98.05	98.11	98.08	98.08
*Exochus*_8_Ich200	95.74	96.19	94.36	94.36	94.38	98.05	98.11	98.08	98.08

	*Exochus_izbus*_Venezuela	*Exochus_izbus*_FG	*Exochus_izbus*_URUGUAY	*Exochus_izbus*_PERU_JU	*Exochus_izbus_2*	*Exochus_jacintus_3*	*Exochus_jacintus*_FG	*Exochus_jacintus*_PERU_JU	*Exochus_tegularis*_Martinique
*Exochus*_12	95.69	95.75	95.75	95.75	94.46	93.91	93.91	93.28	95.44
*Exochus*_Uruguay	96.49	96.52	96.52	96.36	95.11	95.28	95.28	94.5	96.2
*Exochus*_63_Ich98	94.94	95	95	94.84	93.55	93.17	93.17	92.39	94.69
*Exochus*_63_Ich115	94.94	95	95	94.84	93.55	93.17	93.17	92.39	94.69
*Exochus*_63_Ich140	94.94	95.02	95.02	94.86	93.55	93.19	93.19	92.41	94.7
*Exochus_izbus*_1	100	100	100	100	98.7	96.77	96.77	96.13	99.67
*Exochus_izbus*_Guatemala	100	100	100	99.84	98.7	96.88	96.88	96.11	99.69
*Exochus_izbus*_CR	100	100	100	99.84	98.7	96.84	96.84	96.04	99.68
*Exochus_izbus*_PERU_MD	100	100	100	99.84	98.7	96.84	96.84	96.04	99.68
*Exochus_izbus*_Venezuela		100	100	99.84	98.7	96.84	96.84	96.04	99.68
*Exochus_izbus*_FG	100		100	99.84	98.7	96.88	96.88	96.11	99.69
*Exochus_izbus*_URUGUAY	100	100		99.84	98.7	96.88	96.88	96.11	99.69
*Exochus_izbus*_PERU_JU	99.84	99.84	99.84		98.7	96.73	96.73	96.11	99.53
*Exochus_izbus*_2	98.7	98.7	98.7	98.7		95.81	95.81	95.81	99.02
*Exochus_jacintus*_3	96.84	96.88	96.88	96.73	95.81		100	97.97	96.57
*Exochus_jacintus*_FG	96.84	96.88	96.88	96.73	95.81	100		97.97	96.57
*Exochus_jacintus*_PERU_JU	96.04	96.11	96.11	96.11	95.81	97.97	97.97		95.79
*Exochus_tegularis*_Martinique	99.68	99.69	99.69	99.53	99.02	96.57	96.57	95.79	
*Exochus_tegularis*_Saint_Lucia	100	100	100	99.84	98.7	96.88	96.88	96.11	99.69
*Exochus*_1_5	99.04	99.06	99.06	98.9	97.72	97.51	97.51	96.73	98.74
*Exochus*_1_1_PERU_CY	99.04	99.04	99.04	98.87	97.72	97.45	97.45	96.66	98.71
*Exochus*_1_2_PERU_PA	99.04	99.05	99.05	98.9	97.72	97.5	97.5	96.72	98.74
*Exochus*_5_4	98.4	98.43	98.43	98.27	97.07	96.88	96.88	96.11	98.11
*Exochus*_5_2_PERU_MD	98.4	98.43	98.43	98.27	97.07	96.88	96.88	96.11	98.11
*Exochus*_5.1_PERU_UC	98.4	98.42	98.42	98.26	97.07	96.88	96.88	96.09	98.11
*Exochus*_5_3_French_Guyana	98.72	98.74	98.74	98.58	97.39	97.19	97.19	96.41	98.42
*Exochus*_4_8	97.92	97.96	97.96	97.96	97.39	96.41	96.41	95.78	98.27
*Exochus*_4_25_PERU_CU	98.07	98.07	98.07	97.91	98.39	96.49	96.49	95.69	98.39
*Exochus*_4.44_PERU_CY	98.07	98.07	98.07	97.91	98.39	96.49	96.49	95.69	98.39
*Exochus*_4.5_PERU_CU	98.08	98.08	98.08	97.92	97.39	96.51	96.51	95.71	98.4
*Exochus*_4.6_PERU_CU	98.08	98.08	98.08	97.92	97.39	96.51	96.51	95.71	98.4
*Exochus*_4.26_PERU_PA	98.08	98.11	98.11	97.96	97.39	96.56	96.56	95.78	98.43
*Exochus*_7.1_PERU_MD	98.08	98.11	98.11	97.95	97.39	96.55	96.55	95.77	98.42
*Exochus*_7.2_PERU_UC	98.08	98.11	98.11	97.96	97.39	96.56	96.56	95.78	98.43
*Exochus*_8_Ich141	98.08	98.11	98.11	97.96	97.39	96.56	96.56	95.78	98.43
*Exochus*_8_Ich142	98.08	98.11	98.11	97.96	97.39	96.56	96.56	95.78	98.43
*Exochus*_8_Ich200	98.08	98.11	98.11	97.96	97.39	96.56	96.56	95.78	98.43

	*Exochus_tegularis*_Saint_Lucia	*Exochus*_1_5	*Exochus*_1_1_PERU_CY	*Exochus*_1_2_PERU_PA	*Exochus*_5_4	*Exochus*_5_2_PERU_MD	*Exochus*_5.1_PERU_UC	*Exochus*_5_3_French_Guyana	*Exochus*_4_8
*Exochus*_12	95.75	95.75	95.66	95.74	95.13	95.13	95.11	95.43	95.74
*Exochus*_Uruguay	96.52	97.15	97.11	97.15	96.52	96.52	96.52	96.84	96.03
*Exochus*_63_Ich98	95	95	94.9	95	94.38	94.38	94.38	94.69	94.2
*Exochus*_63_Ich115	95	95	94.9	95	94.38	94.38	94.38	94.69	94.2
*Exochus*_63_Ich140	95.02	95.02	94.9	95	94.39	94.39	94.38	94.69	94.22
*Exochus_izbus*_1	100	99.02	99.02	99.02	98.37	98.37	98.37	98.7	98.05
*Exochus_izbus*_Guatemala	100	99.06	99.04	99.05	98.43	98.43	98.42	98.74	97.96
*Exochus_izbus*_CR	100	99.04	99.04	99.04	98.4	98.4	98.4	98.72	97.92
*Exochus_izbus*_PERU_MD	100	99.04	99.04	99.04	98.4	98.4	98.4	98.72	97.92
*Exochus_izbus*_Venezuela	100	99.04	99.04	99.04	98.4	98.4	98.4	98.72	97.92
*Exochus_izbus*_FG	100	99.06	99.04	99.05	98.43	98.43	98.42	98.74	97.96
*Exochus_izbus*_URUGUAY	100	99.06	99.04	99.05	98.43	98.43	98.42	98.74	97.96
*Exochus_izbus*_PERU_JU	99.84	98.9	98.87	98.9	98.27	98.27	98.26	98.58	97.96
*Exochus_izbus*_2	98.7	97.72	97.72	97.72	97.07	97.07	97.07	97.39	97.39
*Exochus_jacintus*_3	96.88	97.51	97.45	97.5	96.88	96.88	96.88	97.19	96.41
*Exochus_jacintus*_FG	96.88	97.51	97.45	97.5	96.88	96.88	96.88	97.19	96.41
*Exochus_jacintus*_PERU_JU	96.11	96.73	96.66	96.72	96.11	96.11	96.09	96.41	95.78
*Exochus_tegularis*_Martinique	99.69	98.74	98.71	98.74	98.11	98.11	98.11	98.42	98.27
*Exochus_tegularis*_Saint_Lucia		99.06	99.04	99.05	98.43	98.43	98.42	98.74	97.96
*Exochus*_1_5	99.06		100	100	99.37	99.37	99.37	99.68	98.27
*Exochus*_1_1_PERU_CY	99.04	100		100	99.36	99.36	99.36	99.68	98.23
*Exochus*_1_2_PERU_PA	99.05	100	100		99.37	99.37	99.37	99.68	98.26
*Exochus*_5_4	98.43	99.37	99.36	99.37		100	100	99.68	97.64
*Exochus*_5_2_PERU_MD	98.43	99.37	99.36	99.37	100		100	99.68	97.64
*Exochus*_5.1_PERU_UC	98.42	99.37	99.36	99.37	100	100		99.68	97.63
*Exochus*_5_3_French_Guyana	98.74	99.68	99.68	99.68	99.68	99.68	99.68		97.95
*Exochus*_4_8	97.96	98.27	98.23	98.26	97.64	97.64	97.63	97.95	
*Exochus*_4_25_PERU_CU	98.07	98.39	98.39	98.39	97.75	97.75	97.75	98.07	99.84
*Exochus*_4.44_PERU_CY	98.07	98.39	98.39	98.39	97.75	97.75	97.75	98.07	99.84
*Exochus*_4.5_PERU_CU	98.08	98.4	98.39	98.4	97.76	97.76	97.76	98.08	99.84
*Exochus*_4.6_PERU_CU	98.08	98.4	98.39	98.4	97.76	97.76	97.76	98.08	99.84
*Exochus*_4.26_PERU_PA	98.11	98.43	98.39	98.42	97.8	97.8	97.79	98.11	99.84
*Exochus*_7.1_PERU_MD	98.11	98.42	98.39	98.42	97.79	97.79	97.79	98.11	99.84
*Exochus*_7.2_PERU_UC	98.11	98.43	98.39	98.42	97.8	97.8	97.79	98.11	99.21
*Exochus*_8_Ich141	98.11	98.43	98.39	98.42	97.8	97.8	97.79	98.11	99.84
*Exochus*_8_Ich142	98.11	98.43	98.39	98.42	97.8	97.8	97.79	98.11	99.84
*Exochus*_8_Ich200	98.11	98.43	98.39	98.42	97.8	97.8	97.79	98.11	99.84

	*Exochus*_4_25_PERU_CU	*Exochus*_4.44_PERU_CY	*Exochus*_4.5_PERU_CU	*Exochus*_4.6_PERU_CU	*Exochus*_4.26_PERU_PA	*Exochus*_7.1_PERU_MD	*Exochus*_7.2_PERU_UC	*Exochus*_8_Ich141	*Exochus*_8_Ich142	*Exochus*_8_Ich200
*Exochus*_12	95.65	95.65	95.67	95.67	95.74	95.73	95.11	95.74	95.74	95.74
*Exochus*_Uruguay	96.13	96.13	96.15	96.15	96.19	96.19	96.19	96.19	96.19	96.19
*Exochus*_63_Ich98	94.25	94.25	94.29	94.29	94.36	94.36	94.36	94.36	94.36	94.36
*Exochus*_63_Ich115	94.25	94.25	94.29	94.29	94.36	94.36	94.36	94.36	94.36	94.36
*Exochus*_63_Ich140	94.25	94.25	94.29	94.29	94.38	94.36	94.38	94.38	94.38	94.38
*Exochus_izbus*_1	98.05	98.05	98.05	98.05	98.05	98.05	98.05	98.05	98.05	98.05
*Exochus_izbus*_Guatemala	98.07	98.07	98.08	98.08	98.11	98.11	98.11	98.11	98.11	98.11
*Exochus_izbus*_CR	98.07	98.07	98.08	98.08	98.08	98.08	98.08	98.08	98.08	98.08
*Exochus_izbus*_PERU_MD	98.07	98.07	98.08	98.08	98.08	98.08	98.08	98.08	98.08	98.08
*Exochus_izbus*_Venezuela	98.07	98.07	98.08	98.08	98.08	98.08	98.08	98.08	98.08	98.08
*Exochus_izbus*_FG	98.07	98.07	98.08	98.08	98.11	98.11	98.11	98.11	98.11	98.11
*Exochus_izbus*_URUGUAY	98.07	98.07	98.08	98.08	98.11	98.11	98.11	98.11	98.11	98.11
*Exochus_izbus*_PERU_JU	97.91	97.91	97.92	97.92	97.96	97.95	97.96	97.96	97.96	97.96
*Exochus_izbus*_2	97.39	97.39	97.39	97.39	97.39	97.39	97.39	97.39	97.39	97.39
*Exochus_jacintus*_3	96.49	96.49	96.51	96.51	96.56	96.56	96.56	96.56	96.56	96.56
*Exochus_jacintus*_FG	96.49	96.49	96.51	96.51	96.56	96.56	96.56	96.56	96.56	96.56
*Exochus_jacintus*_PERU_JU	95.69	95.69	95.71	95.71	95.78	95.77	95.78	95.78	95.78	95.78
*Exochus_tegularis*_Martinique	98.39	98.39	98.4	98.4	98.43	98.42	98.43	98.43	98.43	98.43
*Exochus_tegularis*_Saint_Lucia	98.07	98.07	98.08	98.08	98.11	98.11	98.11	98.11	98.11	98.11
*Exochus*_1_5	98.39	98.39	98.4	98.4	98.43	98.42	98.43	98.43	98.43	98.43
*Exochus*_1_1_PERU_CY	98.39	98.39	98.39	98.39	98.39	98.39	98.39	98.39	98.39	98.39
*Exochus*_1_2_PERU_PA	98.39	98.39	98.4	98.4	98.42	98.42	98.42	98.42	98.42	98.42
*Exochus*_5_4	97.75	97.75	97.76	97.76	97.8	97.79	97.8	97.8	97.8	97.8
*Exochus*_5_2_PERU_MD	97.75	97.75	97.76	97.76	97.8	97.79	97.8	97.8	97.8	97.8
*Exochus*_5.1_PERU_UC	97.75	97.75	97.76	97.76	97.79	97.79	97.79	97.79	97.79	97.79
*Exochus*_5_3_French_Guyana	98.07	98.07	98.08	98.08	98.11	98.11	98.11	98.11	98.11	98.11
*Exochus*_4_8	99.84	99.84	99.84	99.84	99.84	99.84	99.21	99.84	99.84	99.84
*Exochus*_4_25_PERU_CU		100	100	100	100	100	99.35	100	100	100
*Exochus*_4.44_PERU_CY	100		100	100	100	100	99.35	100	100	100
*Exochus*_4.5_PERU_CU	100	100		100	100	100	99.36	100	100	100
*Exochus*_4.6_PERU_CU	100	100	100		100	100	99.36	100	100	100
*Exochus*_4.26_PERU_PA	100	100	100	100		100	99.37	100	100	100
*Exochus*_7.1_PERU_MD	100	100	100	100	100		99.37	100	100	100
*Exochus*_7.2_PERU_UC	99.35	99.35	99.36	99.36	99.37	99.37		99.37	99.37	99.37
*Exochus*_8_Ich141	100	100	100	100	100	100	99.37		100	100
*Exochus*_8_Ich142	100	100	100	100	100	100	99.37	100		100
*Exochus*_8_Ich200	100	100	100	100	100	100	99.37	100	100	

Appendix 10. Matrix of genetic distances for wingless sequences. Numbers indicate genetic similarity as a percentage of shared bases among respective taxa; i.e lower values indicate greater genetic distances.

	*Exochus*_12	*Exochus*_Uruguay	*Exochus*_63_Ich98	*Exochus_izbus*_PERU_JU	*Exochus*_8_Ich141	*Exochus*_8_Ich142	*Exochus*_8_Ich200
*Exochus*_12		95.1	84.43	86.6	90.43	90.19	95.22
*Exochus*_Uruguay	95.1		84.62	85.12	90.12	89.88	99.88
*Exochus*_63_Ich98	84.43	84.62		84.04	85.45	85.45	84.51
*Exochus_izbus*_PERU_JU	86.6	85.12	84.04		84.29	84.29	85.24
*Exochus*_8_Ich141	90.43	90.12	85.45	84.29		99.76	90
*Exochus*_8_Ich142	90.19	89.88	85.45	84.29	99.76		89.76
*Exochus*_8_Ich200	95.22	99.88	84.51	85.24	90	89.76	

CHAPTER IV: Investigating the correlation between elevational range and niche overlap in the parasitoid wasps of the *Exochus albiceps* species-group (Hymenoptera: Ichneumonidae: Metopiinae)

INTRODUCTION

Ichneumonid parasitoid wasps (Hymenoptera) are among the most diverse, widely distributed, and ecologically important groups of terrestrial organisms. The patterns of distribution of Ichneumonidae have attracted the attention of many researchers mainly because they were thought to constitute a classic example of a taxon with an anomalous latitudinal diversity gradient (Owen & Owen 1974). However, this unusual trend may be partly the result of biases in species sampling (Quicke 2012, 2014, Veijalainen *et al.* 2012, Veijalainen *et al.* 2014, Gómez *et al.* 2018), as most taxonomic works pertain to species from temperate regions (Santos & Quicke 2011) and no extensive studies of the family have been conducted in tropical areas, like South America (Sääksjärvi *et al.* 2004, Veijalainen *et al.* 2012). A factor that may influence greatly the diversity of Ichneumonidae at low latitudes is the presence of montane regions. The low-latitude mountains have received little attention, and the spatial distribution of species across tropical altitudinal gradients suggests that mid and high elevations house generally higher ichneumonid species richness and diversity than low-elevation sites, and the majority of species are encountered at mid-elevational ranges (Veijalainen *et al.* 2014).

The *Exochus albiceps* species-group is a monophyletic group of metopiine ichneumonids (Chapter III), including eleven species: *E. ablatus* Gauld & Sithole, 2002 and *E. albiceps* Walsh, 1873, *E. izbus* Gauld & Sithole, 2002, *E. jacintus* Gauld & Sithole, 2002, *E. tegularis* Ashmead, 1894, *Exochus* 1 sp. nov., *Exochus* 2 sp. nov., *Exochus* 4 sp. nov.,

Exochus 5 sp. nov., *Exochus* 7 sp. nov., and *Exochus* 8 sp. nov. The complex generally exhibits a considerable degree of morphological conservatism, but can be characterized by mandibles that are strongly tapered to a fine point and apically twisted, so that when the mandibles are closed they appear more or less unidentate and needle-sharp; the lack of an occipital carina; a distinct sternaulus extending about 0.3× length of the mesosternum; and a propodeum generally with anterior and posterior transverse carinae well defined as well as longitudinal carinae (Chapter III).

The species of the *albiceps* species-group are among the most commonly encountered ichneumonids in the Neotropical region (Gauld & Sithole 2002, Chapter III). The complex is predominantly Neotropical, with one species inhabiting the Nearctic region (Townes 1972, Chapter III). Some species (e.g., *Exochus* 4 sp. nov.) have highly restricted ranges over the complex geographic topography of the neotropics (Chapter III), while others are widely distributed (e.g., *E. izbus*). However, the species-group in general has a wide elevational range, spanning between sea level and 2875m, and richness peaking at sea level to 1500m (Chapter III), with most of the species occurring in wet lowlands (eight species) and a few reaching to mid and high elevations (three species). The distribution of the species makes them an ideal candidate to study the abiotic factors influencing their distributions.

Species niche breadth describes the suite of environments or resources, in the broadest sense, that a taxon can inhabit or use (Gaston *et al.* 1997). By utilizing a greater array of resources and maintaining viable populations within a wider variety of conditions, a species should become more widespread, this would lead to a positive correlation between niche breadth and geographical range size (Brown 1984). High elevation insects are predicted to have wider elevational ranges than low elevation species, because seasonal temperature range tends to increase with elevation (Stevens 1992). Thus, high elevation species may require broader thermal tolerances than lowland species, which also adapts them for wider

elevational ranges (Stevens 1992). However, studies have also shown evidence for high-elevation endemism and narrow elevational ranges in tropical montane species (Garcia-Robledo *et al.* 2016). Together these variable findings suggest that there may be considerable variation in elevational specialization across taxa and geographic locations (Macedo *et al.* 2017).

Elevational ranges of tropical insects along elevational gradients have rarely been explicitly analyzed with most studies focusing on species richness gradients or the shifting of ranges over time (see references in Laurance *et al.* 2011). Here we employ climate-based modelling of species' niches to estimate the level of niche overlap between species within the *E. albiceps* species-group, seeking to elucidate the relationship between elevational range and niche breadth on the speciation processes.

MATERIAL AND METHODS

Locality data and geographical distribution

Distributional data. The occurrence records for the species was obtained from specimens previously examined in the detailed taxonomic revision of the species-group *albiceps*, which presents thorough evaluation of its species geographic distributions (Chapter III) and complemented with a literature review (De Melo *et al.* 2015, Gauld & Sithole 2002, Townes 1972). Historical records lacking geographic coordinates were georeferenced via consultation of Global Gazetteer (http://www.fallingrain.com/world/) and Google Earth (http://www.earth.google.com). Despite the sampling effort, species of this genus are extremely rare in the field and in collections, known from small series of specimens and restricted distribution (Chapter IIII). With these considerations, we analysed six of 11 known species within the species group and compiled a total of 211 locality records (Appendix 11) for the species that were reasonably well-sampled geographically (van Proosdij *et al.* 2016):

93 of *E. izbus*, 30 of *E. jacintus*, 13 records of *Exochus* 1 sp. nov., 24 of *Exochus* 4 sp. nov., 20 of *Exochus* 5 sp. nov., and 17 of *Exochus* 7 sp. nov. The following figure shows the elevational range for each species taken into account, based on the data gathered in Chapter III.

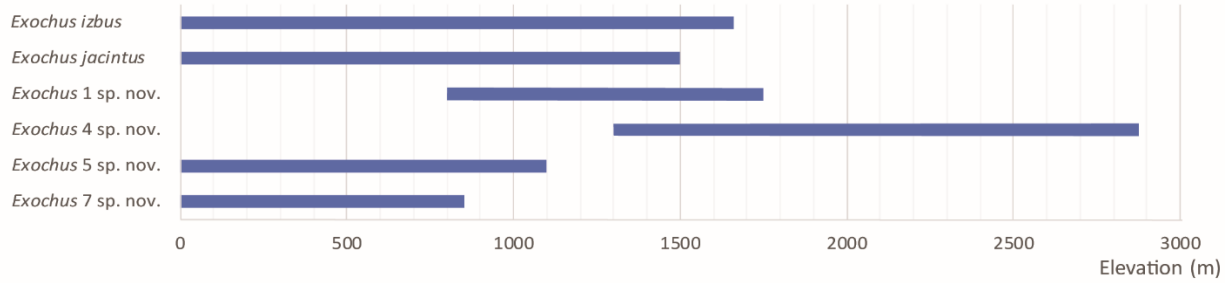

Figure 45. Elevation range per species.

Environmental data

Environmental data were obtained from WorldClim (version 1.3, http://www.world-clim.org; for details, see Hijmans *et al.* 2005). WorldClim contains climate data (i.e., monthly precipitation, and monthly mean, minimum, and maximum temperatures) at a spatial resolution of 2.5' (ca. 5 x 5 km resolution), obtained by interpolation among climate-station records from 1950 to 2000. These data were used to derive biologically meaningful bioclimatic variables representing annual trends, seasonality, and extreme conditions (Hijmans *et al.* 2005). Precipitation and temperature have been found as important environmental variables related to the activity of Ichneumonoidea in tropical forests (González-Moreno *et al.* 2012), and that many ichneumonids have a narrow physiological thermal tolerance (Veijalainen *et al.* 2014). Thus, to characterize the environmental hypervolume of ichneumonid species in our study, we employed four environmental layers: maximum temperature of warmest month (Bio 5), minimum temperature of coldest month (Bio 6), precipitation of wettest month (Bio 13), and precipitation of driest month (Bio 14).

Niche overlap

To test niche overlap we employed two R packages, NicheROVER (Lysy *et al*. 2014) and Hypervolume (Blonder *et al.* 2014). NicheROVER defines the niche region as the joint probability density function of the multidimensional niche indicators at a user-defined probability alpha (e.g., $\alpha = 95\%$). Uncertainty is accounted for in a Bayesian framework, and the method can be extended to three or more indicator dimensions. The overlap metric is the probability that a randomly drawn individual from species A will be found within the niche region of species B (for a given niche region size, e.g., alpha = .95). The overlap is approximated stochastically by generating nprob draws from the distribution of species A and counting the fraction of them which fall in the niche region of species B, where the true values of A and B are estimated from the data. Here the percentage of niche overlap was calculated using 95% niche regions between each pair of species (and 99% for comparison purposes).

The Hypervolume package allows for the fitting of kernel densities to points and uses those kernels to estimate volume and overlap (Blonder *et al.* 2014). For each species, we used their respective spatial points to extract values from the four environmental layers used to describe the environmental niche of species of the genus, using the function *extract* available in the R package *raster* (Hijmans *et al.* 2015). Extracted values were assembled and used to estimate environmental hypervolume for each species. As suggested by the protocols in Blonder et al. (2016), each hypervolume was constructed using a Silverman bandwidth estimator and a 0% quantile threshold with 1000 Monte Carlo samples per data point. The bandwidth axis was estimated for each axis individually, using the estimate bandwidth function, which measures the trade-off between variance in the data and sample size (Blonder *et al.* 2016). After finding the intersection between the two hypervolumes, overlap values were calculated between individual pairs of taxa (2× shared volume/summed volume)

(Blonder *et al.* 2014). The environmental hypervolumes, requires a minimum of three distributional data per species, species with less data were excluded from analysis (Simões *et al*. 2017).

RESULTS

Both analyses show a strong overlap among on the environmental niche of *E. izbus, E. jacintus, Exochus* 5 sp. nov., and *Exochus* 7 sp. nov. The hypervolume calculations (Figs. 46, 47) of *E. izbus, E. jacintus, Exochus* 5 sp. nov., and *Exochus* 7 sp. nov., show a high degree of overlap; while *Exochus* 4 sp. nov. overlaps less with these species. The specimens of *Exochus* 4 sp. nov. occupied different niche spaces (Fig. 46), and this may reflect difficulties in circumscribing this species, with individuals from different elevations perhaps representing separate, cryptic species of relatively recent divergence. Samples are few for this species and extensive further sampling is needed in order to determine whether this species as presently defined is polytypic or is composed of multiple taxa with distinct ecological and evolutionary trajectories. At present, the available material does not permit further elaboration of the challenges posed by this species.

The niche of *Exochus jacintus* overlaps with *E. izbus* and *Exochus* 1 sp. nov. almost completely (1.0, see Fig. 47), it also overlaps slightly less with *Exochus* 7 sp. nov.; while *Exochus* 7 sp. nov. and *Exochus* 5 sp. nov. also overlap almost completely (1.0). Some specimens of *Exochus* 4 sp. nov. overlap less with the other species (although some individuals form a separate environmental hypervolume space that overlaps with the other species), and in general the species does not overlap with *Exochus* 5 sp. nov. (0.0). *Exochus* 5 sp. nov. overlaps slightly less with *Exochus* 1 sp. nov. There is a high posterior distribution overlap (Fig. 48, Table 2) between *E. izbus, E. jacintus, Exochus* 5 sp. nov., and *Exochus* 7 sp. nov. *E. izbus* overlaps with all of the species, and this species has the widest geographical

and elevational distribution (Fig 45). *E. izbus* and *E. jacintus* share the highest posterior distribution of overlap at 95% (93.23) and 99% (97.74), and *E. jacintus* is also widely distributed. *Exochus* 1 sp. nov. and *Exochus* 4 sp. nov. have the least posterior distribution of overlap with species from lowlands.

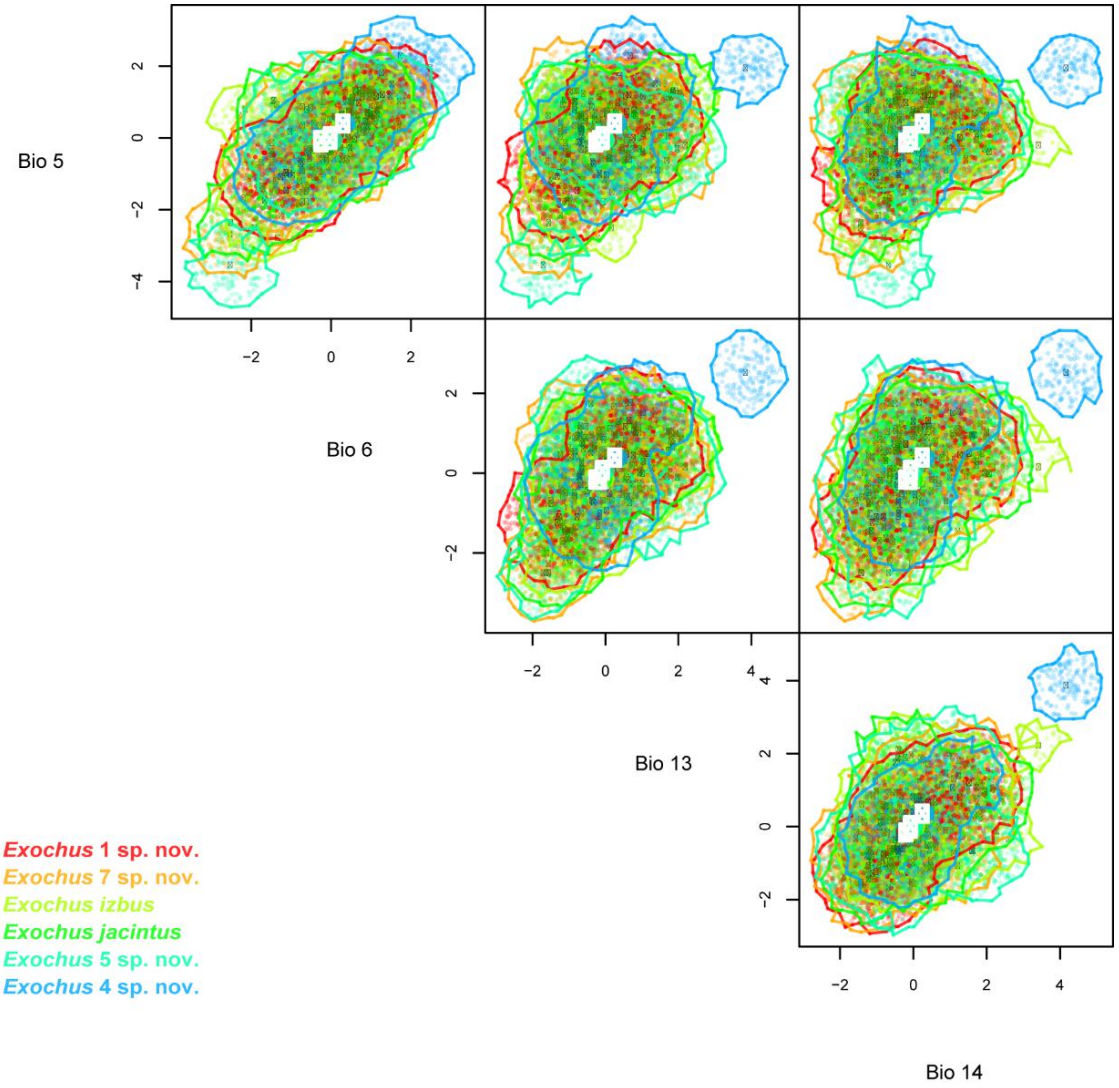

Figure 46. Environmental hypervolumes of species, each showing a degree of overlap across the taxa considered.

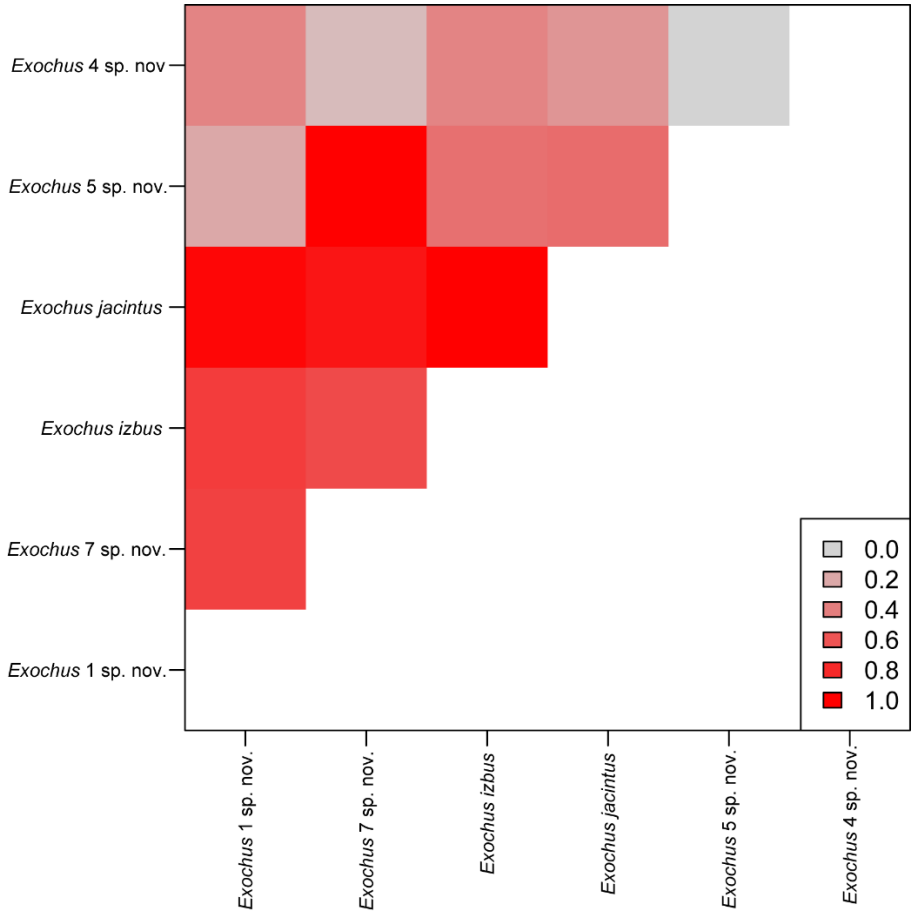

Figure 47. Environmental hypervolumes overlap values calculated between individual pairs of taxa.

Table 2. Niche overlap plots for 95% and 99% niche region size

alpha = 95%

	***Exochus* 1 sp. nov.**	***Exochus* 7 sp. nov.**	***E. izbus***	***E. jacintus***	***Exochus* 5 sp. nov.**	***Exochus* 4 sp. nov.**
***Exochus* 1 sp. nov.**		44.10	74.98	66.84	10.10	53.17
***Exochus* 7 sp. nov.**	1.51		83.88	79.99	60.46	2.36
E. izbus	1.09	43.95		78.61	37.04	1.36
E. jacintus	1.31	57.44	93.23		47.03	1.80
***Exochus* 5 sp. nov.**	0.50	80.28	90.56	83.88		0.67
***Exochus* 4 sp. nov.**	30.54	16.93	34.90	30.55	3.31	

alpha = 99%

	***Exochus* 1 sp. nov.**	***Exochus* 7 sp. nov.**	***E. izbus***	***E. jacintus***	***Exochus* 5 sp. nov.**	***Exochus* 4 sp. nov.**
***Exochus* 1 sp. nov.**		55.24	85.58	78.86	18.99	66.75
***Exochus* 7 sp. nov.**	2.61		91.54	88.89	73.69	5.03
E. izbus	1.93	56.38		89.44	51.40	2.86
E. jacintus	2.30	70.58	97.74		61.59	3.66
***Exochus* 5 sp. nov.**	1.20	89.93	96.29	92.2		2.12
***Exochus* 4 sp. nov.**	41.27	23.92	49.79	43.46	5.64	

The bioclimatic variables (Fig. 49, Table 3) Bio 5 and Bio 6 show similar distributions for *E. izbus*, *E. jacintus*, *Exochus* 5 sp. nov., and *Exochus* 7 sp. nov., and in each case with a narrow range (Fig. 49). These same variables have lower values for *Exochus* 1 sp. nov. and *Exochus* 4 sp. nov. The variables Bio 13 and Bio 14 have a more spread distribution among the species. A lower value for Bio 13 is found in *Exochus* 4 sp. nov., followed by *Exochus* 1 sp. nov.; while Bio 14 has a similar distribution among *Exochus* 5 sp. nov. and *Exochus* 7 sp. nov. and among *E. izbus* and *E. jacintus.* In general, *Exochus* 4 sp. nov. exhibits a lower range for the four variables (Table 3), meaning that the species prefers lower temperatures and precipitation, but this species produced two different hypervolumes and is in need of further exploration as it is likely not a natural taxon as currently circumscribed.

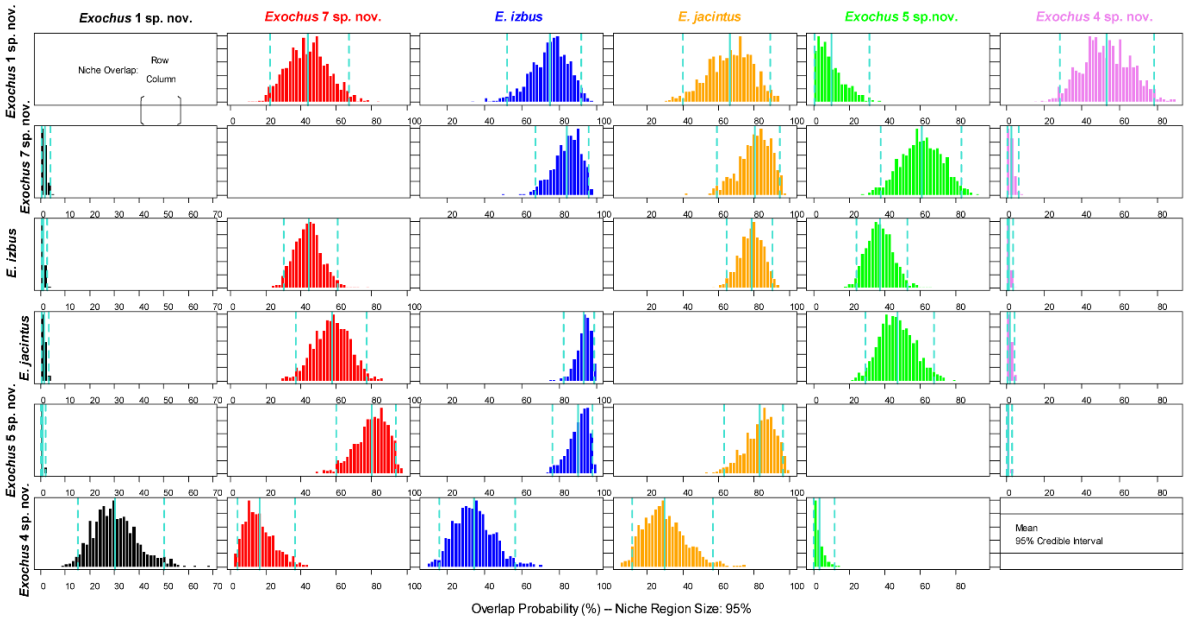

Figure 48. Posterior distribution overlap of 95% nice region among species. Niche overlap is defined as probability from one species (rows) within the niche region of a second species (columns).

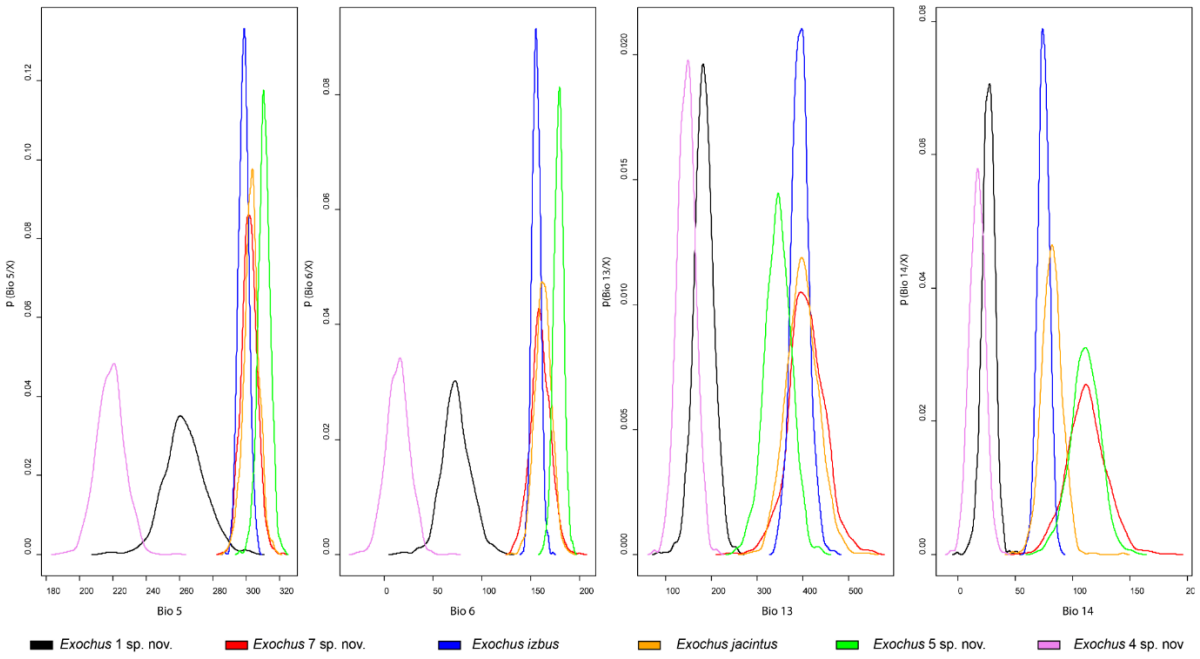

Figure 49. Bioclimatic variables breath per specie

Table 3. Mean (± SD) for the bioclimatic variables per species.

	Bio 5	**Bio 6**	**Bio 13**	**Bio 14**
Exochus izbus	298.85 (± 29.07)	155.42 (± 41.65)	393.81 (± 182.12)	74.47 (± 48.58)
Exochus jacintus	302.93 (± 25.77)	162.28 (± 46.76)	398.66 (± 186.7)	81.79 (± 48.6)
***Exochus* 1 sp. nov.**	262.69 (± 44.21)	73.08 (± 52.21)	182.77 (± 75.3)	26.31 (± 19.71)
***Exochus* 4 sp. nov.**	218.46 (± 38.28)	13.92 (± 54.78)	46.13 (± 90.89)	16.88 (± 31.7)
***Exochus* 5 sp. nov.**	311.00 (± 16.67)	178.30 (± 16.66)	348.15 (± 125.01)	110.70 (± 55.66)
***Exochus* 7 sp. nov.**	302.18 (± 19.41)	159.65 (± 41.9)	406.71 (± 165.51)	111.59 (± 68.89)

DISCUSSION

This study provided some insight into the abiotic variables influencing the niche occupied by the species of the *albiceps* species-group. As expected, there is a clear differentiation between the niche occupied by the lowland species and the montane species. This result concurs with Veijalainen *et al.*'s (2014) suggestion that many ichneumonid species have a narrow physiological thermal tolerance and are specialized for life at specific elevations.

High-elevation insects are predicted to have wider niche ranges than low-elevation species, because seasonal temperature range tends to increase with elevation (Stevens 1992). Thus, high-elevation species may require broader thermal tolerances than lowland species, which also adapts them for wider elevational ranges (Stevens 1992). This seem to be the case for the two montane species investigated, *Exochus* 1 sp. nov. and *Exochus* 4 sp. nov. show a broad breath for variables Bio 5 and Bio 6, both of which are related to temperature (Fig. 49). *Exochus* 1 sp. nov. and *Exochus* 4 sp. nov. are clearly different in their ecological space, which is also evidenced by differences in their elevation zones occupied (Fig. 45). *Exochus* 1 sp. nov. is confined to the elevation range between 850 and 1750m; while *Exochus* 4 sp. nov. to the elevation range between 1300 and 2875m. However, *Exochus* 4 sp. nov. was found to have two different environmental hypervolumes suggesting that the individuals included within the analyses are not all conspecific. Specimens from lower evelations may not be conspecific with those from higher elevations. Presently, insufficient material and collecting localities are available to explore this in greater depth and new material from the habitats harboring these populations are needed in order to look into the genetic diversity of these populations and whether they comprise two cryptically similar species but with different ecological niches. Hosts are also unknown for these species and the degree to which there is host specialization within given elevational ranges or certain geographic areas needs to be explored.

The lowland species, *E. izbus, E. jacintus, Exochus* 5 sp. nov., and *Exochus* 7 sp. nov., occupied similar ecological spaces (the bioclimatic variables Bio 13 and Bio 14 show some differences among the species), which is also evidenced by more or less similar geographical ranges (Figs. 31, 33, 36, 44). Collectively, these species occur widely in the neotropics, especially *E. izbus* (Fig. 31) which has the widest geographical range of the clade; but the

other three species have narrower individual geographical ranges suggesting some degree of disjunct distribution. Due to the different amount of occurrence data among the species (e.g., *E. izbus* is known from 93 separate localities while *Exochus* 7 sp. nov. is known only from 17 localities), it is possible that the analyses lacked sufficient resolving power to discern signals partitioning the niches among these species. Alternatively, climatic variables may not be distinguishing features in these cases and instead host use may drive differences among these species.

When sampling tropical communities of Ichneumonidae, a large proportion of the species are typically represented by singletons and doubletons (Veijalainen *et al.* 2012), as well as low numbers of distinct localities where taxa are found to occur. For example, considering the most recent paper published on Metopiinae (Araujo *et al.* 2018), which includes the description of two new species of *Scolomus*, one of the species is known only from the holotype, and other species is known from three localities. The low occurrence data is a limiting factor when employing niche modelling methods, as many species are rare and known from few localities. Another factor influencing the low occurrence data is the distribution of the species. There are species that occur only at a few, often generally inaccessible localities. *Exochus* 8 sp. nov. is an example of this kind of distribution; it occurs in primary cloud forest of Chanchamayo, Peru, where there are no access roads, so it is likely that this species has a wider distribution than reported but exploring this area is logistically difficult. Thus, at present patterns of distribution and abundance have to be interpreted with considerable caution as the lack of information represents a significant bias in our ability to resolve patterns among most lineages of parasitoid wasps. Accordingly, broadscale generalizations regarding the ecological diversity of parasitoids need to be tempered by the reality of our available data and the need for more extensive sampling.

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APPENDICES

Appendix 11. Ocurrance data per species of the *Exochus albiceps* species-group

Species	Longitud	Latitud
Exochus ablatus	-82.249	8.744
Exochus ablatus	-83.964	10.137
Exochus albiceps	-92.278	30.795
Exochus albiceps	-82.621	35.052
Exochus albiceps	-75.014	39.976
Exochus izbus	-53.874	-34.091
Exochus izbus	-56.347	-32.646
Exochus izbus	-55.533	-27.300
Exochus izbus	-52.383	-27.183
Exochus izbus	-52.383	-27.183
Exochus izbus	-54.617	-25.517
Exochus izbus	-49.198	-24.091
Exochus izbus	-43.955	-22.923
Exochus izbus	-43.292	-22.917
Exochus izbus	-47.239	-22.408
Exochus izbus	-51.714	-17.881
Exochus izbus	-64.815	-17.109
Exochus izbus	-67.216	-15.496
Exochus izbus	-70.389	-13.433
Exochus izbus	-71.108	-13.210
Exochus izbus	-70.347	-12.985
Exochus izbus	-69.379	-12.956
Exochus izbus	-69.384	-12.921
Exochus izbus	-69.370	-12.919
Exochus izbus	-70.960	-12.906
Exochus izbus	-71.321	-12.854
Exochus izbus	-73.196	-12.172
Exochus izbus	-73.053	-11.693
Exochus izbus	-71.411	-11.209
Exochus izbus	-75.399	-11.208
Exochus izbus	-75.404	-11.207
Exochus izbus	-75.398	-11.206
Exochus izbus	-74.909	-10.846
Exochus izbus	-75.389	-10.386
Exochus izbus	-75.188	-10.085
Exochus izbus	-75.031	-7.889
Exochus izbus	-75.664	-7.878
Exochus izbus	-75.314	-7.831
Exochus izbus	-78.485	-5.341
Exochus izbus	-78.980	-4.120
Exochus izbus	-54.433	-2.683
Exochus izbus	-79.762	-1.430
Exochus izbus	-79.203	-0.718
Exochus izbus	-79.350	-0.600
Exochus izbus	-76.500	-0.500
Exochus izbus	-77.070	-0.454
Exochus izbus	-77.028	-0.444
Exochus izbus	-78.775	0.211
Exochus izbus	-52.156	4.544
Exochus izbus	-83.675	8.507
Exochus izbus	-83.350	8.550
Exochus izbus	-83.505	8.566

Species	Longitud	Latitud
Exochus izbus	-83.670	8.618
Exochus izbus	-83.633	8.622
Exochus izbus	-83.389	8.681
Exochus izbus	-83.483	8.683
Exochus izbus	-82.250	8.733
Exochus izbus	-83.300	8.750
Exochus izbus	-83.400	8.767
Exochus izbus	-83.283	8.767
Exochus izbus	-82.637	8.771
Exochus izbus	-82.962	8.787
Exochus izbus	-83.681	8.788
Exochus izbus	-82.400	8.800
Exochus izbus	-82.793	8.891
Exochus izbus	-83.421	8.897
Exochus izbus	-82.867	8.950
Exochus izbus	-83.008	9.029
Exochus izbus	-83.008	9.029
Exochus izbus	-79.872	9.219
Exochus izbus	-79.917	9.267
Exochus izbus	-82.883	9.583
Exochus izbus	-69.667	9.633
Exochus izbus	-82.817	9.650
Exochus izbus	-83.853	9.763
Exochus izbus	-84.478	10.091
Exochus izbus	-83.964	10.137
Exochus izbus	-83.917	10.151
Exochus izbus	-63.640	10.200
Exochus izbus	-84.553	10.232
Exochus izbus	-84.797	10.277
Exochus izbus	-67.683	10.350
Exochus izbus	-67.966	10.396
Exochus izbus	-84.009	10.431
Exochus izbus	-84.017	10.433
Exochus izbus	-85.467	10.933
Exochus izbus	-85.433	11.000
Exochus izbus	-91.194	14.550
Exochus izbus	-88.033	14.950
Exochus izbus	-89.144	15.403
Exochus izbus	-87.458	15.734
Exochus izbus	-93.450	16.883
Exochus izbus	-95.067	18.567
Exochus izbus	-100.163	25.362
Exochus izbus	-84.796	10.304
Exochus izbus	-84.648	10.777
Exochus izbus	-83.283	8.759
Exochus izbus	-83.459	9.818
Exochus jacintus	-55.789	-26.681
Exochus jacintus	-49.553	-22.291
Exochus jacintus	-70.951	-13.074
Exochus jacintus	-71.669	-13.072
Exochus jacintus	-70.924	-13.011
Exochus jacintus	-70.347	-12.985

Species	Longitud	Latitud
Exochus jacintus	-69.367	-12.972
Exochus jacintus	-71.411	-11.209
Exochus jacintus	-75.399	-11.208
Exochus jacintus	-75.404	-11.207
Exochus jacintus	-75.398	-11.206
Exochus jacintus	-74.909	-10.846
Exochus jacintus	-73.863	-8.414
Exochus jacintus	-79.170	-0.340
Exochus jacintus	-53.294	3.367
Exochus jacintus	-52.217	4.600
Exochus jacintus	-52.217	4.667
Exochus jacintus	-83.675	8.507
Exochus jacintus	-83.573	8.539
Exochus jacintus	-83.505	8.566
Exochus jacintus	-83.483	8.683
Exochus jacintus	-82.817	9.650
Exochus jacintus	-67.687	10.348
Exochus jacintus	-84.017	10.433
Exochus jacintus	-83.701	10.461
Exochus jacintus	-61.314	10.662
Exochus jacintus	-61.400	10.683
Exochus jacintus	-61.287	10.691
Exochus jacintus	-85.433	11.000
Exochus jacintus	-69.379	-12.956
Exochus tegularis	-61.200	13.250
Exochus tegularis	-60.983	14.017
Exochus tegularis	-61.010	14.478
Exochus tegularis	-61.042	14.490
Exochus 1 sp. nov.	-71.556	-13.208
Exochus 1 sp. nov.	-71.569	-13.194
Exochus 1 sp. nov.	-71.569	-13.192
Exochus 1 sp. nov.	-71.603	-13.114
Exochus 1 sp. nov.	-71.550	-13.083
Exochus 1 sp. nov.	-71.556	-13.081
Exochus 1 sp. nov.	-73.187	-12.703
Exochus 1 sp. nov.	-73.184	-12.694
Exochus 1 sp. nov.	-72.962	-12.359
Exochus 1 sp. nov.	-73.183	-12.320
Exochus 1 sp. nov.	-73.053	-12.311
Exochus 1 sp. nov.	-75.512	-11.130
Exochus 1 sp. nov.	-75.303	-10.756
Exochus 2 sp. nov.	-43.955	-22.923
Exochus 2 sp. nov.	-41.185	-20.604
Exochus 4 sp. nov.	-71.589	-13.281
Exochus 4 sp. nov.	-71.589	-13.279
Exochus 4 sp. nov.	-71.635	-13.254
Exochus 4 sp. nov.	-71.715	-13.254
Exochus 4 sp. nov.	-71.633	-13.253
Exochus 4 sp. nov.	-71.714	-13.253
Exochus 4 sp. nov.	-71.598	-13.243
Exochus 4 sp. nov.	-71.597	-13.242
Exochus 4 sp. nov.	-71.595	-13.241
Exochus 4 sp. nov.	-72.706	-13.229
Exochus 4 sp. nov.	-71.536	-13.197

Species	Longitud	Latitud
Exochus 4 sp. nov.	-71.569	-13.194
Exochus 4 sp. nov.	-71.583	-13.183
Exochus 4 sp. nov.	-71.595	-13.176
Exochus 4 sp. nov.	-72.755	-13.123
Exochus 4 sp. nov.	-71.687	-13.113
Exochus 4 sp. nov.	-71.594	-13.108
Exochus 4 sp. nov.	-71.594	-13.108
Exochus 4 sp. nov.	-71.156	-13.081
Exochus 4 sp. nov.	-71.556	-13.080
Exochus 4 sp. nov.	-73.500	-12.850
Exochus 4 sp. nov.	-73.187	-12.703
Exochus 4 sp. nov.	-75.297	-10.756
Exochus 4 sp. nov.	-71.645	-13.311
Exochus 5 sp. nov.	-52.141	4.546
Exochus 5 sp. nov.	-53.269	3.778
Exochus 5 sp. nov.	-67.216	-15.496
Exochus 5 sp. nov.	-70.347	-12.985
Exochus 5 sp. nov.	-71.028	-12.983
Exochus 5 sp. nov.	-71.419	-12.893
Exochus 5 sp. nov.	-71.321	-12.854
Exochus 5 sp. nov.	-71.297	-12.761
Exochus 5 sp. nov.	-71.232	-12.655
Exochus 5 sp. nov.	-72.848	-12.344
Exochus 5 sp. nov.	-72.845	-12.344
Exochus 5 sp. nov.	-72.989	-12.150
Exochus 5 sp. nov.	-73.813	-8.412
Exochus 5 sp. nov.	-78.606	-5.298
Exochus 5 sp. nov.	-73.786	-4.268
Exochus 5 sp. nov.	-74.702	-3.210
Exochus 5 sp. nov.	-74.708	-3.201
Exochus 5 sp. nov.	-74.724	-3.198
Exochus 5 sp. nov.	-55.059	5.328
Exochus 5 sp. nov.	-71.204	-12.727
Exochus 7 sp. nov.	-70.849	-13.122
Exochus 7 sp. nov.	-70.865	-13.024
Exochus 7 sp. nov.	-71.589	-13.010
Exochus 7 sp. nov.	-70.347	-12.985
Exochus 7 sp. nov.	-71.069	-12.924
Exochus 7 sp. nov.	-71.914	-12.879
Exochus 7 sp. nov.	-71.321	-12.854
Exochus 7 sp. nov.	-71.236	-12.838
Exochus 7 sp. nov.	-73.183	-12.320
Exochus 7 sp. nov.	-72.700	-11.783
Exochus 7 sp. nov.	-59.721	-11.698
Exochus 7 sp. nov.	-73.798	-8.460
Exochus 7 sp. nov.	-75.503	-3.875
Exochus 7 sp. nov.	-76.820	-2.550
Exochus 7 sp. nov.	-77.673	-1.033
Exochus 7 sp. nov.	-52.251	4.544
Exochus 7 sp. nov.	-52.207	4.559
Exochus 8 sp. nov.	-75.503	-11.193
Exochus 8 sp. nov.	-75.516	-11.127
Exochus 8 sp. nov.	-75.515	-11.119